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PART N, VOLUME 1, CHAPTER 26A: INTRODUCTION TO THE HIPPURITIDA (RUDISTS): SHELL STRUCTURE, ANATOMY, AND EVOLUTION

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INTRODUCTION

The Hippuritida is an extinct monophyletic order of inequivalved, thick-shelled bivalves, which evolved an extraordinary variety of morphologies, including some of the most baroque modifications of the bivalve body plan known to science (Fig. 1). Their vernacular name, rudists, is the anglicized form of the name originally coined by Lamarck (1819), *les rudistes,* from the Latin, *rudis*, meaning rough or uncultivated. The term was used for a motley selection of fossils that included a couple of inarticulate brachiopods (*Crania* Retzius, 1781 and *Discina* Lamarck, 1819) and a lidded coral (*Calceola* Lamarck, 1799) in addition to just two genera of rudists, *Radiolites* Lamarck,1801 and *Sphaerulites* Lamarck, 1819, as currently recognized, together with a rudist internal mold (*Birostrites* Lamarck, 1819). The continued bewilderment of early 19th century paleontologists as to the taxonomic composition and biological affinities of rudists was summarized by Woodward (1855), who was among the first to recognize the natural grouping of bivalves that constitute the rudists as understood today. Usually highly gregarious, the sessile epifaunal rudists colonized shallow seafloors in great abundance on the carbonate sediment-dominated platforms and shelves that developed extensively along the equatorially encircling Tethyan-Atlantic-tropical Pacific oceanic belt of the Late Jurassic and Cretaceous periods (Simo, Scott, & Masse, 1993; Philip, 1998; Skelton, 2003). There, they grew in clusters of varying density, often forming broad shelly meadows (Fig. 2) or low mounds that commonly became preserved as laterally extensive biostromes and bioherms (Gili & Götz, 2018, see *Treatise Online,* Part N, Chapter 26B). Their abundant fossil record depicts an Oxfordian origin with rapid diversification thereafter, especially through middle to Late Cretaceous times. This evolutionary radiation was occasionally checked, however, by episodic mass extinctions that were coupled with carbonate platform crises, terminating in a final catastrophic demise of the group at the close of the Cretaceous Period (Steuber & others, 2016, see T*reatise Online,* Part N, Chapter 26C).

EXTERNAL SHELL FORM AND LIGAMENT

Primitively, both umbos of the rudist shell grew projecting spirogyrally forwards and outwards during growth, like an unequal pair of ram's horns (Fig. 1.1), one of which—according to the clade to which the species belonged—grew at least initially cemented to some hard surface. Spirogyrate shell growth was subsequently retained in all taxa that attached by the left valve (suborder Requieniidina), though increasingly inequivalved development led to the free (right) valve becoming caplike (Fig. 1.2) or even operculiform in some cases. By contrast, early in the evolution of the clade of species

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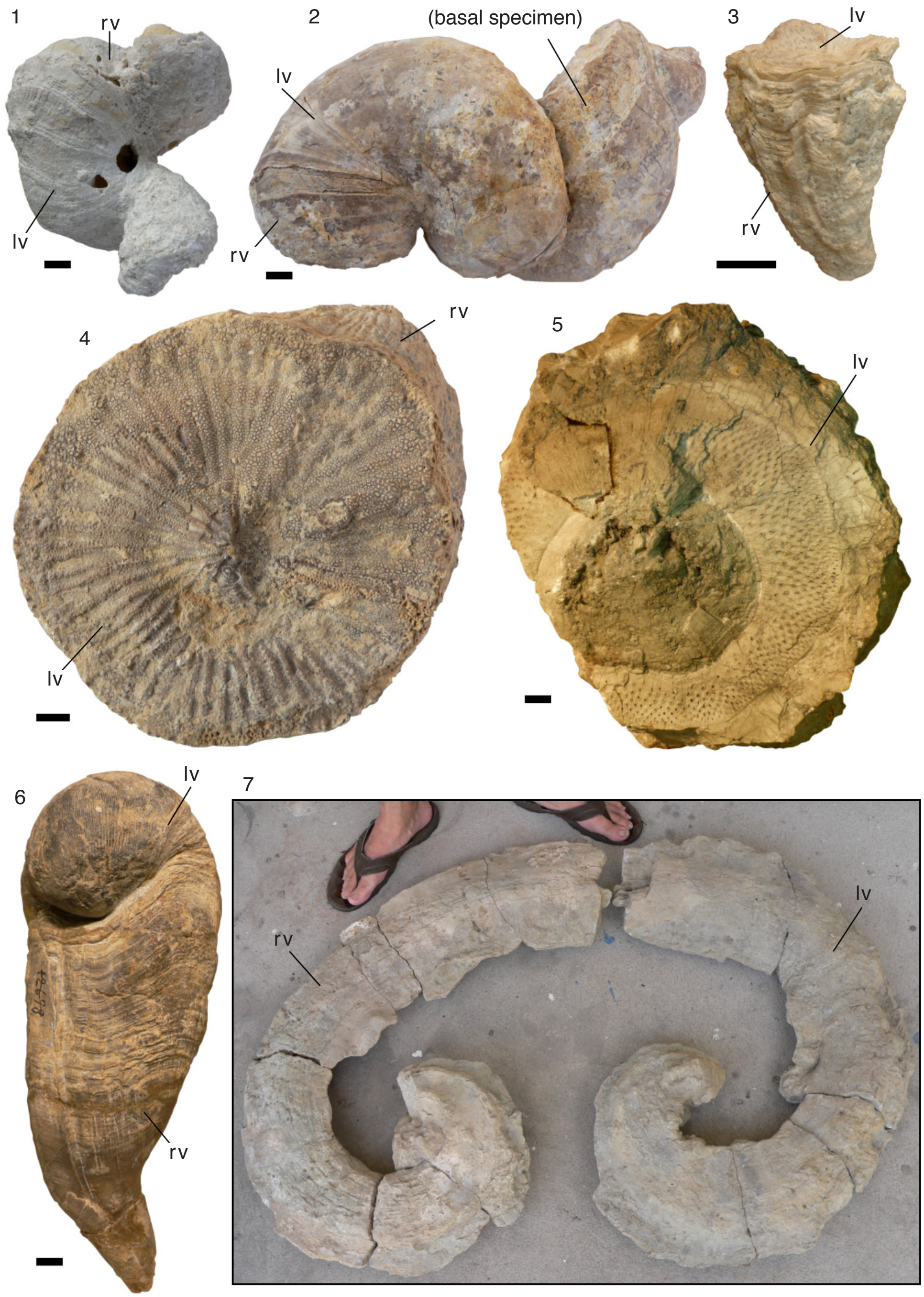

Fig. 1. Morphological diversity in rudists. *1, Epidiceras sinistrum* (Deshayes, 1824) (Epidiceratidae), anterior view of articulated shell, PWS, Oxfordian, Dompcevrin (Meuse), France; *2, Toucasia carinata* (Matheron, 1843) (Requieniidae), posterior view of articulated shell (as from above in life) attached to a second shell, PWS, Aptian, São Julião, Portugal; *3, Agriopleura libanica* (Astre, 1930) (Radiolitidae), postero-ventral view of articulated shell, PWS, Aptian, eastern Saudi Arabia; *4, Pseudovaccinites giganteus major* (Toucas, 1904) (Hippuritidae), view of articulated shell from *(Continued on facing page)*.

that attached by the right valve (suborder Hippuritidina), the valves began to uncoil during growth (as explained below). In these forms, the right valve adopted a more or less elongate, straight, or curved conical to cylindrical form (Fig. 1.3–1.4, 1.6–1.7, Fig. 2.2), while the left valve developed every variation from being operculiform, or gently domed (Fig. 1.3–1.5), to capuloid (Fig. 1.6), or secondarily extended (Fig. 1.7). Such variations in growth geometry were closely linked with the broad palaeoautecological repertoire of rudists (SKELTON, 1985; GILI, MASSE, & SKELTON, 1995; GILI & GÖTZ, 2018; see *Treatise Online,* Part N, Chapter 26B).

FIG. 2. *1,* Diorama of radiolitid meadow on Cenomanian carbonate platform flanking an intraplatform depression, based on exposures in southern Istria, Croatia (artwork by the late John Watson, The Open University, UK; see also Tišlar & others, 1998). *2,* Cluster of *Sauvagesia nicaisei* (COQUAND, 1862) (Radiolitidae) preserved in life position and viewed obliquely from above, upon which the radiolitid meadow (*1*) is based, Frašker Island, southern Istria, Croatia; scale bar, 50 mm (Skelton, 2003, fig. 1.*11* and 1.*13,* respectively).

This diversification of rudist shell forms was enabled by changes in the pattern of ligamentary growth. The primitive external ligament was of modified parivincular type (YONGE, 1967), with the arched fibrous (compressive) component supported in each valve by a robust shelly nymph (Fig. 3.1), similar to that seen, for example, in extant *Arctica islandica* (LINNAEUS, 1767) (Fig. 3.2). However, exaggerated posteriorward growth-migration of the rudist ligament around the curved valve margins caused its anterior end to be split apart continuously as the umbos progressively diverged; the split trail of old ligament in each valve in turn became overgrown by retrograding marginal shell increments (Fig. 3.1). The functional ligamentary zone connecting the two valves thus migrated tangentially backwards throughout growth, such that the umbos became projected outwards, spirogyrally, in front of it (SKELTON, 1978, 1979; Fig. 3.1). In a further modification, within the suborder Hippuritidina, extreme shortening of the functional ligament led to its becoming invaginated from the dorsal margin (Fig. 3.3a–b). Only a vestigial string of fibrous ligament now remained to connect the two valves, continuously splitting apart almost as soon as it was generated (SKELTON, 1979; Fig. 3.4a–c). The invagination of the ligament overcame the primitive constructional constraint of spirogyrate growth, enabling the diverse patterns of uncoiled shell growth described above (SKELTON, 1985). Later, in a

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FIG. 1. *(Continued from facing page).*

above left valve, PWS, Santonian, Collades de Basturs, southern Central Pyrenees, Spain; *5, Joufia reticulata* BOEHM, 1897 (Radiolitidae), partial left valve with outer part broken away to reveal canals in outer shell layer, NHM L93155, Campanian, Monte Jouf, northeast Italy; *6, Coralliochama orcutti* WHITE 1885 (Plagioptychidae), dorsal view of articulated shell, lectotype, USNMNH 186661, Campanian, California, USA; *7, Titanosarcolites giganteus* (WHITFIELD, 1897) (Antillocaprinidae), posterior (upper) view of articulated shell, specimen arranged as seen from above in life position, Maastrichtian, Marchmont Inlier, Jamaica, Department of Geography and Geology Museum, The University of the West Indies, Mona Campus, Kingston, Jamaica; *lv*, left valve; *rv*, right valve; scale bars, *1–6,* 10 mm; *7,* geologist's feet for scale (*1–7,* new).

FIG. 3. Rudist ligaments. *1,* Left valve of *Epidiceras sinistrum* (DESHAYES, 1824), showing site of insertion of active ligament and outer shell layer overgrowth on anterior trace of old, split ligament, NHM LL31920, Oxfordian, Dompcevrin (Meuse), France; *2,* right valve of extant *Arctica islandica* (LINNAEUS, 1767), showing insertion of medially sectioned parivincular ligament, for comparison with (*1*), PWS, South Devon, UK; *3a,* left valve of *Pachytraga tubiconcha* ASTRE, 1961 (Caprinidae), showing site of insertion of invaginated ligament, NHM PI MB 131, Hauterivian of Cabo Raso, Cascais, Portugal; *3b,* close-up view of ligamentary insertion site in *3a*; *4a,* transverse section in adumbonal view of right valve of *Radiolites angeiodes* (DE LAPEIROUSE, 1781) (Radiolitidae), with inserted teeth of left valve, showing invaginated ligamentary string preserved at tip of calcitic *arête cardinale* infolded from outer shell layer, surrounded by aragonitic inner shell (creamy white color), USNMNH 259009, Coniacian, Gosau Beds of Brandenberg Basin, Austria; *4b,* SEM photograph of invaginated ligament of specimen in *4a*, in broken section, showing tip of *arête cardinale* projecting in from upper left and ruptured aragonite fibers of ligament rooted on inner shell at right (posterior side); *4c,* higher magnification view of aragonite fibers of ligament in *4b; am*, anterior myophore; *at*, anterior tooth (left valve); *ct*, central tooth (right valve); *cts*, central tooth socket; *pm*, posterior myophore; *pt*, posterior tooth; scale bars: *1–4a,* 10 mm; *4b,*100 µm; *4c*, 0.5 µm (*1–4a,* new; *4b–4c,* Skelton 1979, fig. 4A & 4E, respectively).

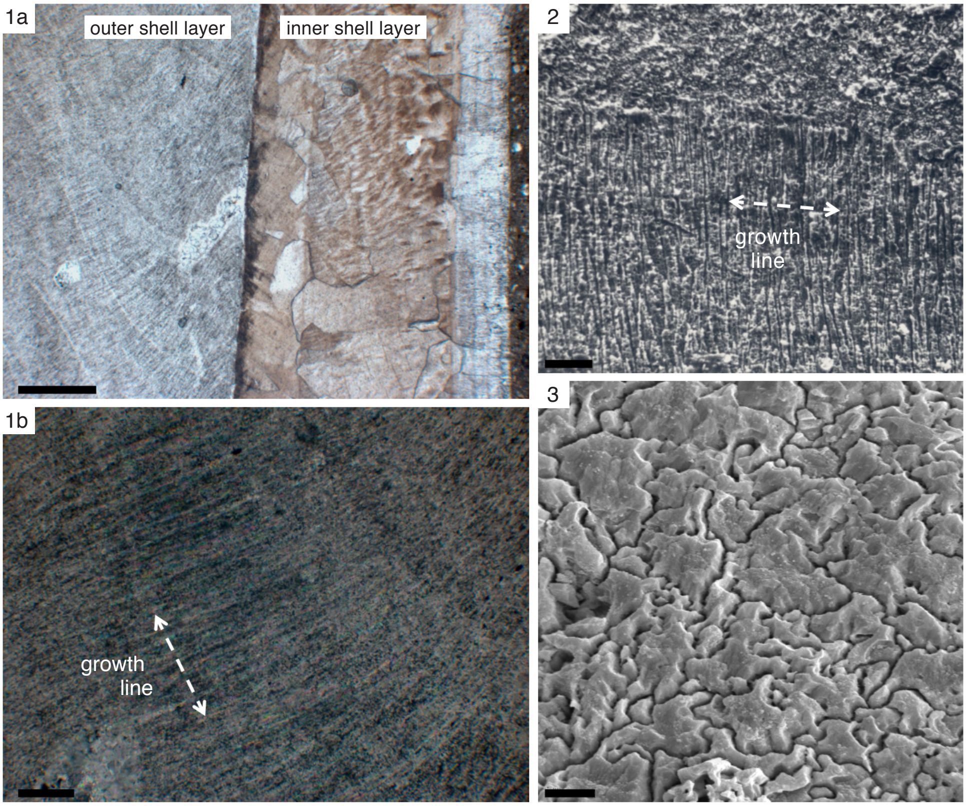

FIG. 4. Rudist shell layers and microstructures. *1a,* Photomicrograph, in plane-polarized light, of thin section of right valve wall in radial section of *Hippurites socialis* Douvillé, 1890a (Hippuritidae), showing fibrous prismatic outer shell layer on the left and originally aragonitic (now paramorphically calcitized) inner shell of crossed-lamellar to complex crossed-lamellar structure with an inner lining of myostracal prisms on the right, PWS, Santonian, Piolenc (Vaucluse), France; *1b,* magnified detail of outer shell layer in *1a,* in crossed-polarized light, revealing acicular fibrous prisms oriented perpendicularly to the growth lines (indicated by *white dashed line*); *2,* SEM photograph of fibrous prisms on underside of radial canal in left valve outer shell layer of *Hippuritella toucasi* (d'Orbigny, 1850) (Hippuritidae), PWS, Santonian, Figuières (Bouches-du-Rhône), France; *3,* SEM photograph of outer surface of outer shell layer in *Hippurites socialis,* showing end-on view of fibrous prisms (i.e., periostracal eye-view), revealing large variability in size and extensive interdigitation of neighboring prisms, same locality as *1a;* scale bars: *1a,* 0.5 mm; *1b,* 0.1 mm; *2,* 20 µm; *3,* 5 µm (*1a–2,* new; *3,* image courtesy of Elizabeth Harper, Cambridge University, UK).

number of relatively derived rudist taxa, the ligament was lost altogether.

SHELL STRUCTURE AND COMPOSITION

All rudists possessed an outer shell layer of fibrous, prismatic, low-magnesium calcite (Skelton & Smith, 2000), with Mg values mostly <4000 ppm and clustering around 2000 ppm (Steuber, 1999a). The needlelike prisms constituting this shell layer lie subparallel to one another, oriented more or less perpendicularly to original growth surfaces, hence to the growth lines seen in section (Fig. 4.1a–b, 4.2). This microstructure appears to have resulted from very low-angle spherulitic growth of the calcite prisms in the outer shell layer, which, according to a recent high-resolution SEM investigation by Harper and Checa (2017), had a very low organic content, allowing a virtually inorganic style of crystallization with intricate lateral interdigitation of neighboring prisms (Fig. 4.3). For this particular kind of fibrous microstructure,

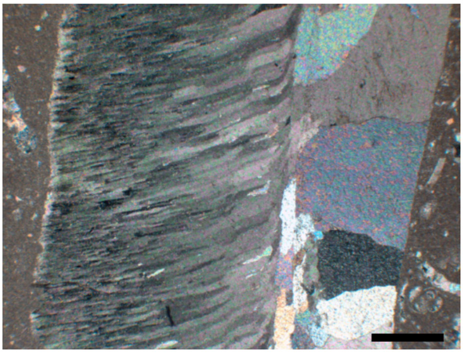

Fig. 5. Diagenesis of rudist shell layers, illustrated in thin section photomicrograph in crossed-polarized light of radial section of left valve wall of *Toucasia carinata* (Matheron, 1843) (Requieniidae). Note calcitic outer shell layer, on left, has undergone lateral aggrading neomorphism of prisms (contrast with pristine acicular prisms in Fig. 4.*1b*), while the originally aragonitic inner shell, on the right, has been entirely replaced by sparry calcite, PWS, Aptian, Crismina Fort, Cascais, Portugal; scale bar, 0.5 mm (new).

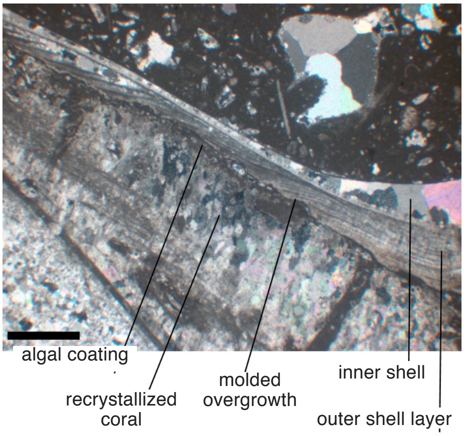

Fig. 6. Role of outer shell layer in rudist shell attachment, illustrated in thin section photomicrograph in crossed-polarized light of radial section of anterior left valve wall of *Toucasia carinata* (Matheron, 1843) (Requieniidae). Note encrusting algally coated coral (below left, recrystallized). Also note molded overgrowth of irregular surface of substrate revealed by undulations of prograding asymptotic growth lines in prismatic outer shell layer, PWS; scale bar, 0.5 mm (Skelton & Gili, 2012, Fig 8D).

Harper and Checa (2017) recommend retention of the descriptive term fibrillar prisms, originally used by Skelton (1976). Diagenetic alteration involving aggrading neomorphism across clusters of prisms may yield more broadly differentiated zones of optical extinction when viewed in cross-polarized light (Fig. 5). However, pristine preservation of the original microstructure and mineralogy is not uncommon, especially in examples of Late Cretaceous age, and has provided excellent material for several isotopic/geochemical and sclerochronological studies (e.g., Steuber, 1999a, 2000; Steuber & Schlüter, 2012, and literature cited therein). In relation to function during growth, one of the principal roles of the calcitic outer shell layer was attachment to hard surfaces (including other individuals), both by settling juveniles and, opportunistically, by adults, as shown by growth lines that reveal asymptotic marginal overgrowth of the substratum (Fig. 6; see also Skelton & Gili, 2012).

Primitively, the calcitic outer shell layer is relatively thin (approximately 1 mm), and usually externally ornamented by thin growth lines and, especially in the attached valve, fine radial riblets (e.g., Fig. 1.1, Fig. 7.1). However, this shell layer varies greatly in thickness amongst more derived forms, reaching up to tens of cm thick in some taxa or being reduced to a thin, sub-millimetric veneer in others. In no case is it known to have been entirely lost. Nevertheless, phyletic changes in its relative thickness that were apparently correlated with long-term fluctuations in seawater temperatures have been documented in some rudist lineages (Pascual-Cebrian & others, 2016).

External ornamentation of the shell ranges from smooth (Fig. 7.2) to strongly costate (Fig. 7.3), with varying development of growth rugae. Annual shell growth rates may

Fig. 7. *(Continued from facing page).*

conjoined specimens of *Caribbea muellerriedi* (Vermunt, 1937) (Hippuritidae), showing partially eroded, porous-roofed radial canal system in outer shell layer of left valve in specimen at right, and radial infoldings of right valve outer shell layer in specimen at left, comprising an *arête cardinale*, flanked by grooves for left valve teeth at bottom of image, and two pillars on the left, USNMNH 187687 (from Norman Sohl acid-etched collection, locality no. 1202), Maastrichtian, Sabana Grande Quadrangle (Municipio de Lajas), Puerto Rico; scale bars: *1, 5,* 0.5 mm; *2,* 5 mm; *3, 4, 6,* 10 mm (*1, 3–6,* new; *2,* Skelton & others, 2010, fig. 6k).

Fig. 7. Diversity in thickness, external ornamentation, and mesostructures of outer shell layer in rudists. *1,* Thin section photomicrograph in plane-polarized light of transverse section of right valve wall of *Pachytraga paradoxa* (Pictet & Campiche, 1869) (Caprinidae), showing fine external ribbing on relatively thin outer shell layer oriented diagonally across middle of image, with spar-replaced inner shell at upper left, PWS, Aptian, Crismina Fort, Cascais, Portugal; *2,* pair of small, articulated specimens of *Polyconites hadriani* Skelton & others, 2010 (Polyconitidae), showing thickened, gray-brown outer shell layer, externally smooth apart from growth rugae, paratypes, NHM PI MB 1018, Aptian, Las Mingachas locality, Miravete de la Sierra (Teruel Province), Spain; *3,* articulated shell of *Durania cornupastoris* (Des Moulins, 1826) (Radiolitidae), showing radial costae on thick outer shell layer of right (lower) valve together with finely ribbed pair of radial bands on its postero-ventral flank, NHM 65170, Turonian, Les Pyles, Dordogne, France; *4,* detail of thick outer shell layer growth surface of right valve in *Lapeirousia jouanneti* (Des Moulins, 1826) (Radiolitidae), showing fine celluloprismatic mesostructure of polygonal cell plan, as well as radially branching mantle vascular impressions, NHM, unregistered, Campanian, Dordogne, France; *5,* thin section photomicrograph in crossed-polarized light of radial section of right valve wall of *Durania* cf. *apula* (Parona, 1900) (Radiolitidae), showing spar-filled cells of celluloprismatic mesostructure, PWS, Maastrichtian, Khashm Hajajah, Al-Aramah Plateau, eastern Saudi Arabia; *6,* acid-etched, silicified cluster of

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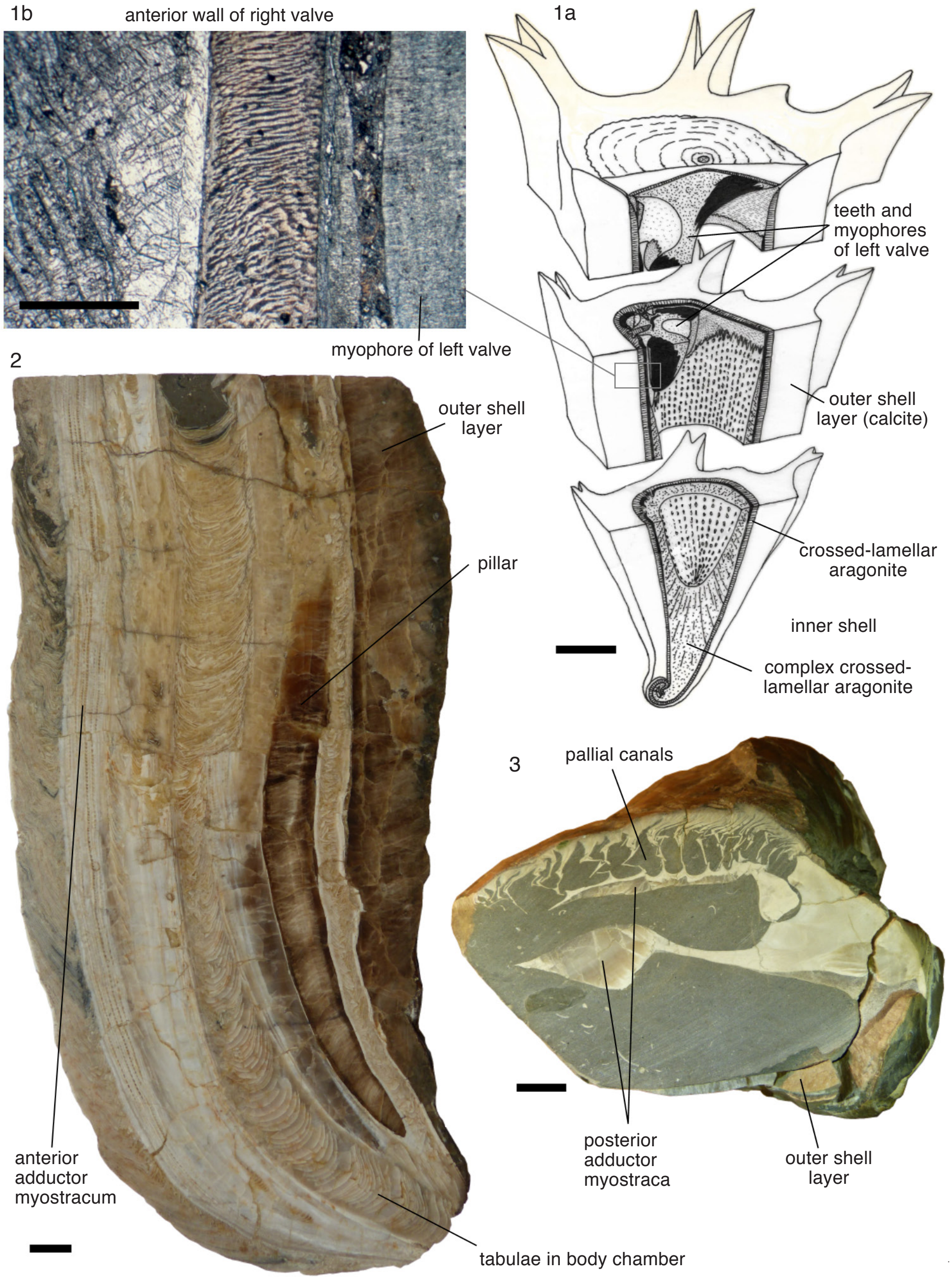

FIG. 8. Aragonitic inner shell of rudists. *1a,* Exploded diagram of shell microstructure distribution in *Biradiolites angulosissimus* TOUCAS, 1909 (Radiolitidae), with anterior part of shell cut away to show radial section, black areas indicate myostraca; *1b,* photomicrograph of acetate peel of area indicated by rectangle in *1a*, showing, from left to right, calcitic outer shell layer (partially crushed and re-crystallized), aragonitic crossed lamellar middle shell layer (striped brown pattern), and opposing aragonitic myostraca of the anterior adductor muscle of right valve wall and left valve myophore, respectively; *2,* radial section of lower part of right valve of *Pseudovaccinites gosaviensis* (DOUVILLÉ, 1890b) (Hippuritidae), recorded as "U. Turonian" (but more likely Santonian), with exceptional partial

(Continued on facing page).

be estimated where spacing of such rugae can be correlated with cyclical stable isotopic (especially O) fluctuations of likely seasonal origin preserved in pristine, thick outer shell layers. Measured values ranged from <10 mm to 44 mm per annum in right valves from various hippuritid and a radiolitid species sampled by STEUBER (2000). If, by analogy, similar periodic growth rugae observed on the thin outer shell layer of some caprinoid rudists with elongate canaliculate valves can likewise be considered annual, then even higher annual growth rates may be inferred. An average annual value of 6.9 mm was noted, for example, in a right valve of *Kimbleia* COOGAN, 1973 by SCOTT (2002).

Distinctive mesostructural modifications of the outer shell layer are characteristic of certain higher taxa. In most (though not all) Radiolitidae, for example, the outer shell layer of at least the right valve, but sometimes both, consists of stacked sheets of tiny cells (celluloprismatic structure; see Terms Used in the Description of Rudist Morphology, p. 29), produced by repeated mm-scale (or finer) wrinkling and roofing over of broad growth surfaces (Fig. 7.4–7.5; see also REGIDOR-HIGUERA, GARCÍA-GARMILLA, & SKELTON, 2007; PONS & VICENS, 2008). In the Hippuritidae, pores on the external surface of the left valve communicate with radial canals in the outer shell layer that open around its inner margin (Fig. 7.6; see also SKELTON, 1976; SCHUMANN, 2010).

The inner shell was originally aragonitic, with crossed lamellar and fine, complex, crossed-lamellar microstructures, but also containing extensive myostracal zones (Fig. 4.1a, Fig. 8.1a–b; KENNEDY & TAYLOR, 1968; SKELTON, 1974, 1976). The inner shell included the myocardinal apparatus, consisting of the teeth and sockets (Fig. 3.4a), and the myophores, on which the adductor muscles were rooted (Fig. 8; SKELTON, 1974, 1976). The original aragonite is rarely preserved as such, usually only in organic-rich clays/marls or glauconitic sandstones (KENNEDY & TAYLOR, 1968; SKELTON, 1974). In some specimens, it has merely undergone neomorphic calcitization, with variable paramorphic preservation of growth lines and/or shell microstructures (Fig. 9.1a–b). More commonly, however, the original aragonite has been entirely leached away, leaving moldic cavities that may be secondarily filled by sparry calcite and with any remaining internal structure preserved only by micrite envelopes (Fig. 9.2). Mesostructural elaborations of the inner shell include blind-ending longitudinal tubes or pallial canals (Fig. 10.1–10.2; see also Terms, p. 29–30) that penetrate from the internal valve surface, as well as "false-floor" tabulae formed within the body cavity and other cavities (Fig. 10.3a–b), including the pallial canals in some forms (e.g., Fig. 10.2). Both pallial canals and tabulae evolved independently in a number of different taxa (SKELTON & SMITH, 2000; SANO & others, 2014).

INTERNAL SHELL FEATURES

DENTITION

The massive, pachyodont dentition of rudists usually comprises three major teeth, two in one valve straddling one in the other. In the primitive dental arrangement, termed normal by DOUVILLÉ (1886, 1887), there is one main tooth in the left valve flanked by two in the right valve (Fig. 11.1–11.2). Early in the evolution of the Hippuritidina, however, shortening of the active ligament was accompanied by transformation of the dentition to a so-called inverse condition

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FIG. 8. *(Continued from facing page)*.
preservation of aragonitic inner shell (creamy-white), including anterior adductor myostracum and tabulae, NHM 33972, Gosau, Austria; *3,* dorso-ventral section through articulated shell of *Plagioptychus aguilloni* (D'ORBIGNY, 1839) (Plagioptychidae), showing myostraca of posterior adductor on opposing myophores as slightly darkened, pale brown areas of aragonitic inner shell, as well as pallial canals in left valve, NHM L. 30151, Santonian, Gosau, Austria; scale bars: *1a,* 5 mm; *1b,* 1 mm; *2–3,* 10 mm (*1a,* adapted from Skelton, 1974, fig. 1; *1b–3,* new).

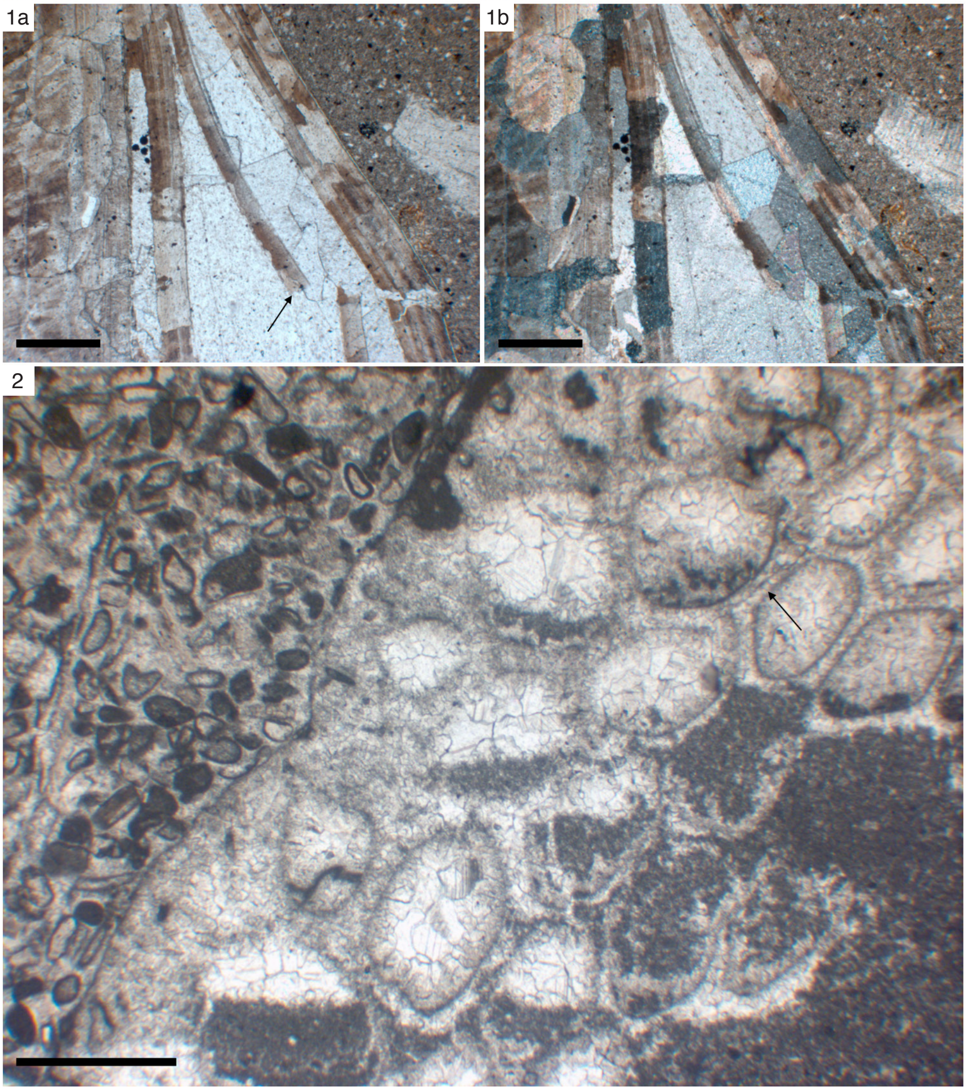

Fig. 9. Diagenesis of rudist inner shell. *1a–b,* Thin section photomicrographs, in plane-polarized and crossed-polarised light respectively, of right valve inner wall, at left, in radial section of *Hippurites socialis* Douvillé, 1890a, with tabulae of body cavity (*arrow* marks pre-cementation fracture) and spar-filled intertabular spaces, differential zones of extinction in *1b* reveal paramorphic calcitization of original complex crossed-lamellar structure, which is ghosted as brown patterning within shell wall and tabulae, PWS, Santonian, Piolenc (Vaucluse), France; *2,* photomicrograph, in plane-polarized light, of thin section across valve fragment of *Ichthyosarcolites* Desmarest, 1812 (Ichthyosarcolitidae), with calcitic outer shell layer missing through erosion, and although original aragonite of canaliculate inner shell was then entirely dissolved away, canal walls have been preserved by a framework of micrite envelopes that had lined them (marked with *arrow*), allowing both primary and secondary pore spaces to be filled subsequently by sparry calcite; some canals also contain geopetal fills of pelletal micrite, PWS, Cenomanian, Ciaulec, Southern Apennines, Italy; scale bars, 0.5 mm (new).

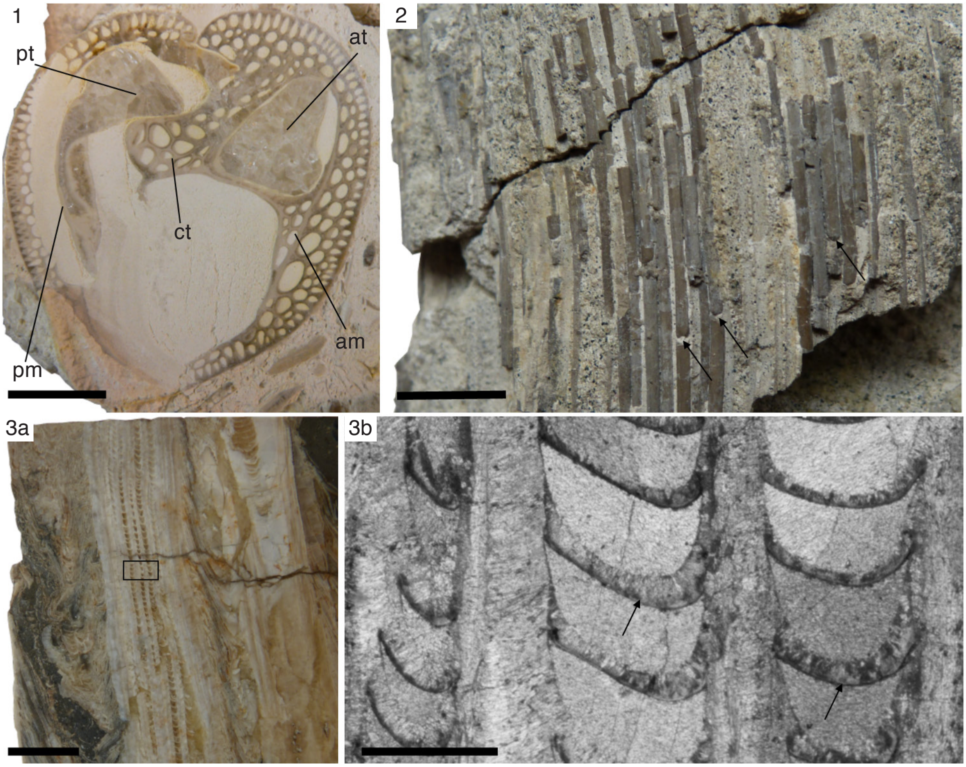

FIG. 10. Pallial canals and tabulae in rudists. *1,* Abumbonal view of transverse section of right valve, with inserted teeth and posterior myophore of left valve of *Caprinuloidea romeri* MITCHELL, 2013a (Caprinuloideidae), showing pallial canals penetrating most of right valve, USNMNH PAL.534223, Albian, Whitney Dam, Texas, USA; *2,* detail of eroded valve surface of *Ichthyosarcolites triangularis* DESMAREST, 1812 (Ichthyosarcolitidae), showing dark cement infills of originally capillary-like pallial canals with spaced interruptions (marked by *arrows*) resulting from dissolution of tabulae within canals, NHM L. 63180, Cenomanian, locality unrecorded, France; *3a,* detail of *Pseudovaccinites gosaviensis* (DOUVILLÉ, 1890b) specimen (shown in Fig. 8.2), showing fine columns of tabulae within trace of anterior myophore, NHM 33972; *3b,* photomicrograph of peel from area of rectangle in *3a*, showing tabulae (marked by *arrows*) between vertical myophoral ridges, both containing myostracal prismatic structure, PWS; *am*, anterior myophore; *at*, anterior tooth; *ct*, central tooth; *pm*, posterior myophore; *pt*, posterior tooth; scale bars: *1–3a,* 10 mm; *3b,* 1 mm (*1,* Mitchell, 2013a, fig. 4A; *2–3b,* new).

(DOUVILLÉ, 1886, 1887), comprising two teeth in the left valve and one in the right valve. This latter change was not, strictly, a true dental inversion, as seen in the living Chamidae, for example. Instead, it came about as a result of progressive evolutionary enlargement of an incipient posterior toothlet situated behind the ligament in the left valve (Fig. 11.1) and suppression of the small anterior tooth in the right valve (Fig. 11.2), as later recognized by DOUVILLÉ (1896; Fig. 11.3–11.4). As a consequence, in uncoiled forms, the invaginated ligament is situated in front of the posterior tooth of the left valve and dorsally with respect to the single right valve tooth and its socket (Fig. 3.3–3.4a), a useful criterion for determining the identity and orientation of valves in otherwise indeterminate specimens. In uncoiled Hippuritidina, the posterior tooth in the left valve is thus primitively much smaller than the anterior tooth (Fig. 11.3a–b), but can be enlarged so as to be subequal or even equal in size to it in more derived forms (Fig. 11.4–11.5). Moreover, certain radiolitids that lack a

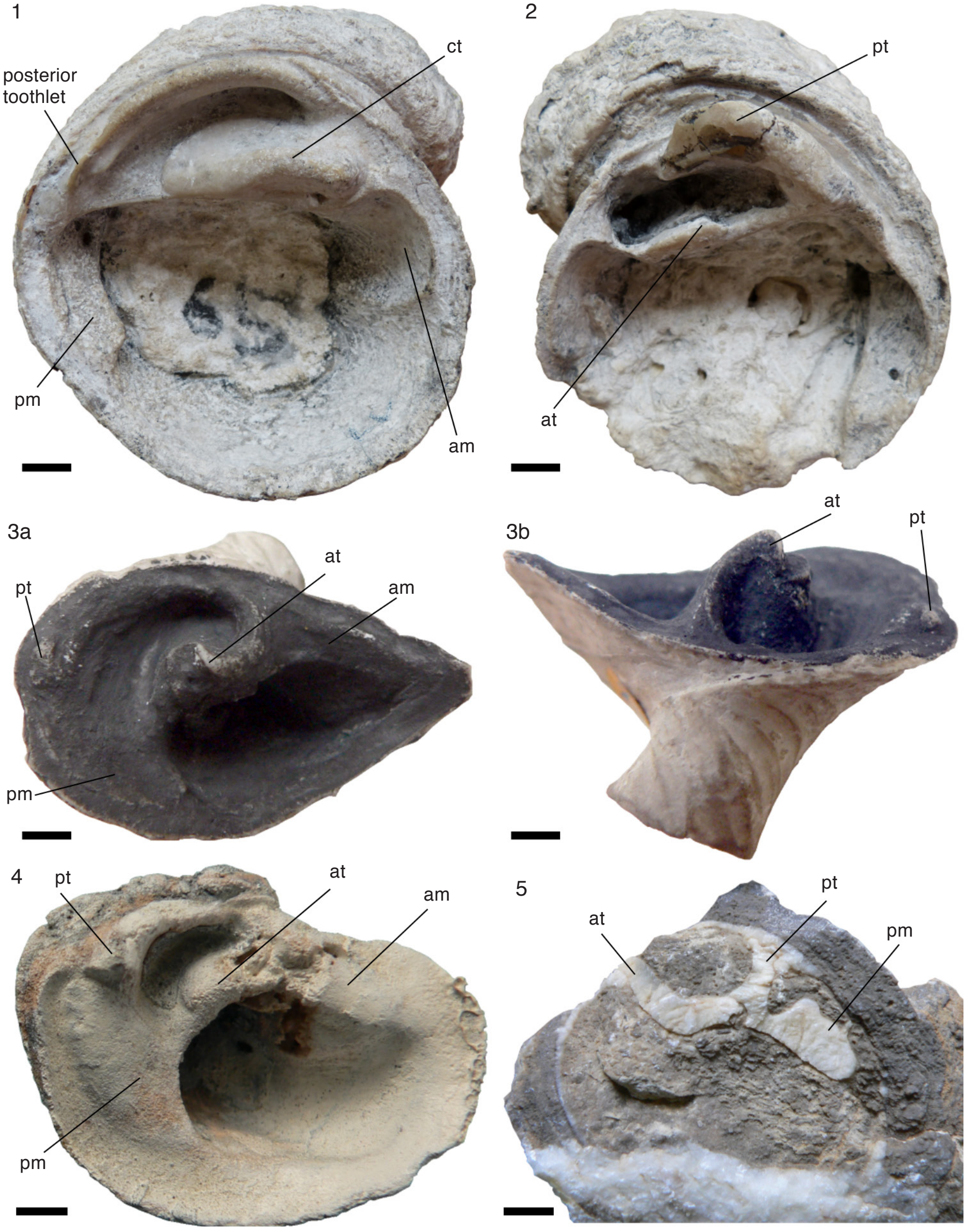

FIG. 11. Rudist dentition. *1–2, Epidiceras sinistrum* (DESHAYES, 1824) (Epidiceratidae), Oxfordian, Dompcevrin (Meuse), France; *1,* left valve, NHM LL31920; *2,* right valve, NHM LL31921, illustrating normal dentition; *3a–b,* left valve of *Valletia antiqua* JOUKOWSKY & FAVRE, 1913 (Diceratidae), in adapical (*3a*) and dorsal (*3b*) views, illustrating primitive, unequal inverse dentition, NHM LL23861, Tithonian, Štramberk, Czech Republic; *4,* left valve of *Monopleura* MATHERON, 1843 (Monopleuridae), illustrating derived, subequal inverse dentition, Early Cretaceous, Darwin Guyot, Mid-Pacific Mountains; *5,* natural transverse section of right valve in adapical view, plus left valve myocardinal arc of *Bournonia tibetica* DOUVILLÉ, 1916 (Radiolitidae), illustrating loss of ligamentary infolding and of central tooth, Nanjing Institute of Geology and Palaeontology, Chinese Academy of Sciences XZGB006, Campanian–Maastrichtian, Tibet; *am*, anterior myophore; *at*, anterior tooth; *ct*, central tooth; *pm*, posterior myophore; *pt*, posterior tooth; scale bars: *1–2,* 10 mm; *3a–b, 4–5,* 5 mm (*1–3, 5,* new; *4,* Skelton, Sano, & Masse, 2013, fig. 5b).

ligament also lose the central tooth of the right valve, such that the left valve teeth are simply seated in grooves in the right valve dorsal wall (Fig. 11.5).

ADDUCTOR MUSCLE INSERTIONS AND MYOPHORES

Myophoral arrangements in rudists are diverse and their systematic usefulness has long been recognized (e.g., Douvillé, 1888, 1889; Mac Gillavry, 1937; Skelton, 2013a). Both the diversification and the subsequent phylogenetic conservatism of myophoral reorientations resulted from constructional compromises between evolving rudist shell growth geometry and the constraint imposed by muscle anchorage in the shell. In living molluscs, attachment of muscles to the shell is mediated by a layer of matted collagen (tendon sheath) secreted by specialized adhesive epithelium, to which the muscle cells, in turn, attach (Tompa & Watabe, 1976; Fig. 12.1). Bonding of the tendon sheath to the shell is secured by bundles of collagen fibers that are embedded in aragonitic myostracal prisms (Fig. 12.2). The muscle fibers, in turn, connect with bundles of fibrils that traverse the specialized epithelium and link with the tendon sheath (Fig. 12.1). The muscle fibers are capable of serial detachment from, and lateral reattachment to the fibrils of the adhesive epithelium. The muscles are thereby able to creep, step-by-step, tangentially across the adhesive epithelium on the inner shell surface during growth, while continuously maintaining secure anchorage (Fig. 12.3). On the other hand, the close adhesion of the tendon sheath to the underlying shell limits the rate of accretionary growth of the myostracum relative to the surrounding inner surface of the shell, as the common indentation of muscle scars on the shell interior testifies. This combination of the facility for tangential muscle migration, on the one hand, with the limitation of underlying myostracal growth, on the other, means that in order for the adductors to maintain their relative anatomical positions within the growing shell, their shell insertions must remain more or less co-planar with the growth trajectories of the muscles across the inner shell surface. In most bivalves, the muscle scars thus lie flush on the inner valve surfaces, spirally tracking the accretionary growth of the valve margins (Fig. 12.3).

Essentially, the same growth geometry was maintained in the early spirogyrate rudists, though with the posterior adductor insertions migrating helicospirally along myophoral ledges that subtended shallowly from the commissural plane in each valve instead of simply tracking across the inner valve wall (Fig. 12.4). The opposing posterior myophoral ledges in the two valves served to reduce the length of the muscle (hence its susceptibility to elastic stretching) across the wide interior span of the globose shell. With further shortening of the adductors, the myophores of both muscles eventually became ventral extensions of the hinge plates (e.g., Fig. 11.3–11.4). As valve growth became increasingly uncoiled, however, the adductor insertion surfaces in the tubular right (lower) valve were constrained to incline more steeply with respect to the commissural plane in order to continue their radial tracking of valve margin growth, necessitating complementary rotation of projecting left valve myophores so as to face them (Fig. 12.5). Different uncoiled clades of rudists adopted contrasting possible options for such myophoral tilting (Fig. 13). Once adopted, however, each arrangement proved effectively irreversible, thereby providing a consistent phylogenetic signal for the clade concerned. For example, in the Caprinidae, the posterior myophore in the left valve tilted inwards (Fig. 13.1a) so as to face onto the back of an erect myophore in the right valve (Fig. 13.1b), which itself projected up across the commissural plane (Fig. 13.1c). In the Caprinuloideidae, by contrast, the left valve posterior myophore tilted the opposite way, outwards (Fig. 13.2), so as to face onto the posterior wall of the right valve (Chartrousse, 1998a). Yet another arrangement arose in the Polyconitidae, in which the left valve posterior myophore projected from a

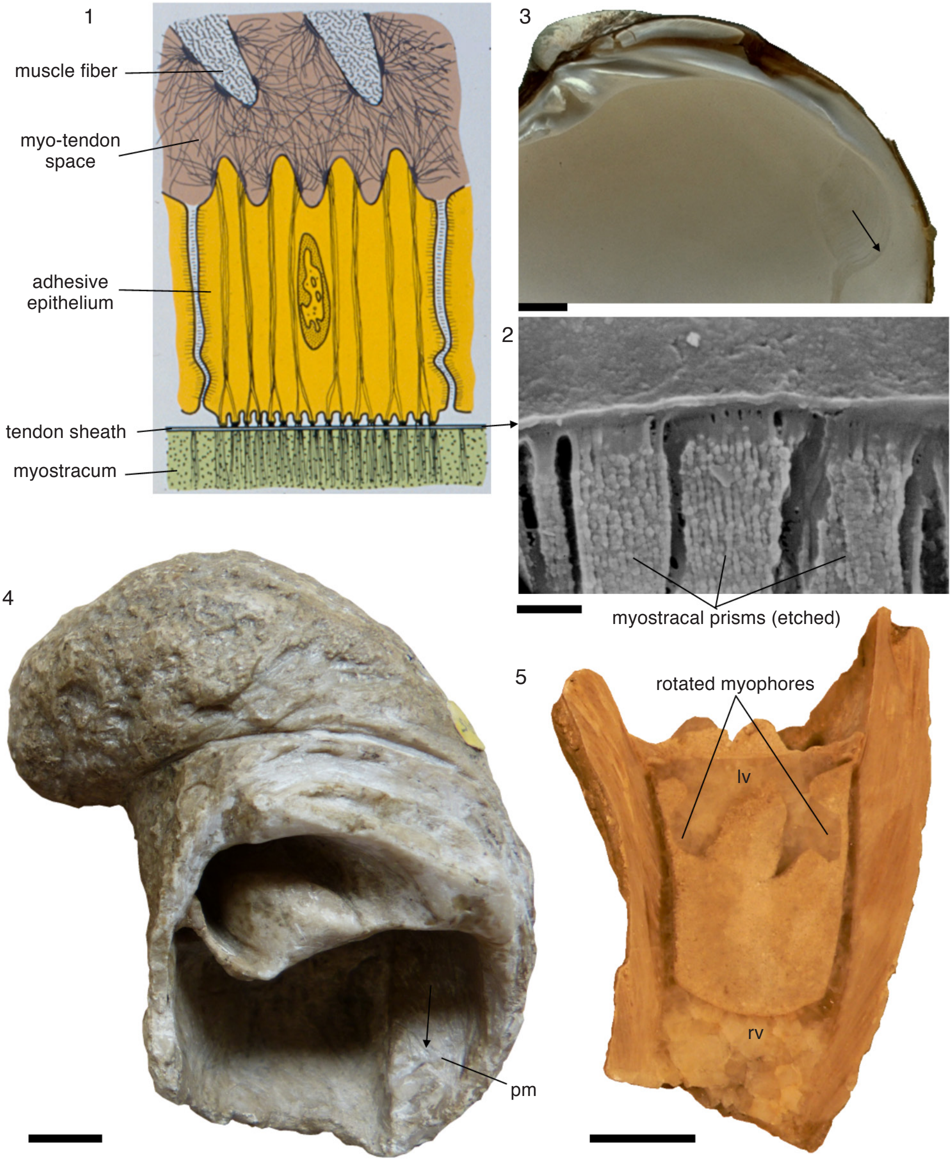

FIG. 12. Adductor muscle insertions and myophores. *1,* Diagram illustrating mode of molluscan muscle-shell attachment via specialized adhesive epithelium (see p. 13 for explanation); *2,* SEM photograph of junction between epoxy-embedded anterior adductor muscle plus adhesive epithelium (undifferentiated area, above) and myostracal prisms of shell (below), etched in 0.5% formic acid for 20 seconds, in extant *Mercenaria mercenaria* (LINNAEUS, 1758), revealing how bundles of collagen fibers emerging from the tendon sheath (marked by *arrow*) are embedded in the myostracal prisms, Maryland, USA (PWS, sample preparation by Don Dean, Department of Paleobiology, USNMNH); *3,* right valve interior of extant *Arctica islandica* (LINNAEUS, 1767) (as in Fig. 3.2), with radial growth trajectory of posterior adductor muscle insertion across inner valve surface indicated by *arrow,* PWS; *4,* right valve of *Diceras arietinum* LAMARCK, 1805 (Diceratidae), showing posterior myophore (*pm*) with growth trajectory of adductor insertion surface indicated by *arrow*, NHM 33915, Oxfordian, Chatel-Censoir (Yonne), France; *5,* antero-posterior radial section of *Eoradiolites davidsoni* (HILL, 1893) (Radiolitidae), showing rotation of left valve (*lv*) myophores to face inner walls of right valve (*rv*), USNMNH 145655, Albian, Texas, USA; scale bars: *2,* 1 µm; *3–5,* 10 mm (*1,* new, adapted from information in Tompa & Watabe, 1976; *2–5,* new).

relatively more internal part of the myocardinal platform and was reflexed back so as to face either inwards onto a low myophoral shelf in the right valve (Fig. 13.3) or outwards onto the posterior wall of the right valve (SKELTON & others, 2010).

FUNCTIONAL ANATOMY

MUSCULAR INSERTIONS

Besides those for the adductor muscles discussed above, other muscle insertion scars and myostraca (or a demonstrable lack of them) in rudists allow further inferences to be made concerning their anatomy—in the absence of any records of exceptional soft-part preservation. Thus, for example, the lack of discrete pedal muscle retractor scars—in contrast to their presence in putative megalodontiform sister taxa—implies loss of the foot even in the earliest rudists (diceratids and epidiceratids) in association with the evolution of attachment to the substratum (SKELTON, 1978), as with extant oysters. On the other hand, the finely preserved internal molds of some small epidiceratids reveal the presence of a short arc of tiny pits on the underside of each hinge plate (Fig. 14.1) corresponding to those produced along the dorso-lateral margin of the visceral mass, including the anterior limit of the gills, in living heterodont bivalves (SKELTON, 1978; Fig. 14.2). By contrast, no distinct pallial line has been located in any rudist. While it might be tempting to interpret the sharply demarcated boundary between the thickened calcitic outer shell layer and the aragonitic inner shell in certain taxa—such as hippuritids and radiolitids—as corresponding to a pallial line, no seam of myostracal prisms is observable along this junction in rare specimens with preserved aragonitic shell microstructures (Fig. 4.1, Fig. 8.1b). However, layers of myostracal prisms can be found in some specimens, lining the deeper shell interior (Fig. 4.1a), including in some cases, the tabulae (Fig. 10.3b). Pallial attachment thus seems to have been situated relatively deeply within the shell, again as in oysters, with no distinct commarginal pallial line present, in turn implying the ability for deep withdrawal of the mantle lobe margins—of clear advantage for an exposed sessile epifaunal life habit.

GAPING AND FEEDING

In those rudists that retained an external ligament (all Requieniidina and the Diceratidae, only, among the Hippuritidina), it can be assumed to have kept its normal function of opening the valves on relaxation of the adductor muscles. Hence these forms may, most parsimoniously, be supposed to have fed by means of gill filtering, as with other suspension-feeding bivalves (Fig. 14.2). Upon invagination, however, the ligament became vestigial (Fig. 3.4a), with any remaining scope for active gaping limited to about a millimeter or less (SKELTON, 1979). Such extreme reduction of gaping is confirmed both by the persistence of a residual, fibrous (hence non-extensible) ligamentary string connecting the valves in the majority of uncoiled taxa in life, indicated by its continuous splitting during growth (Fig. 3.4b–c), and by the extreme shortening of the adductor muscles that accompanied ligamentary invagination (e.g., Fig. 8.1a–b, Fig. 12.5). This limitation of gaping would have inhibited the inhalant/exhalent flow that is typical of most other suspension-feeding bivalves, rendering normal gill filtering unlikely in most if not all uncoiled rudists. In addition, the relatively small size of the mantle cavity in such rudists indicates that their gills became much reduced. At the same time, their inner valve margins became enlarged and elaborated, (e.g., especially, Fig. 1.3–1.5, Fig. 7.3–7.6), suggesting that the function of food particle entrapment may have been taken over from the gills by the expanded mantle margins (SKELTON, 1979). The pore-fed radial canal system in the outer shell layer of the hippuritids (Fig. 1.4, Fig. 7.6, Fig. 15), in particular—already postulated to have channeled respiratory currents by ZAPFE (1937)—can thus readily be interpreted to have served also as a mantle-based filter-feeding system (SKELTON, 1976; SCHUMANN, 2010).

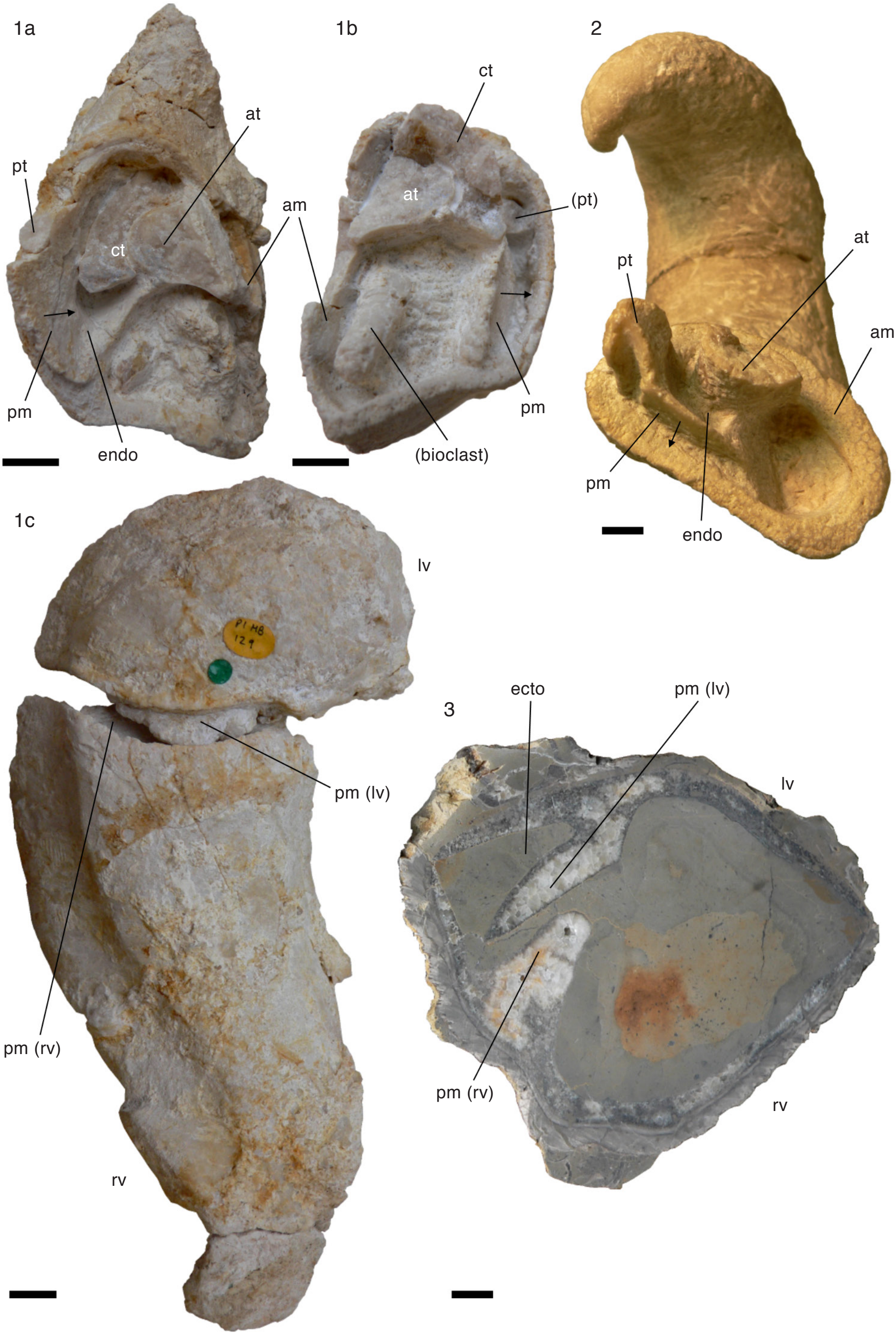

FIG. 13. *(For explanation, see facing page).*

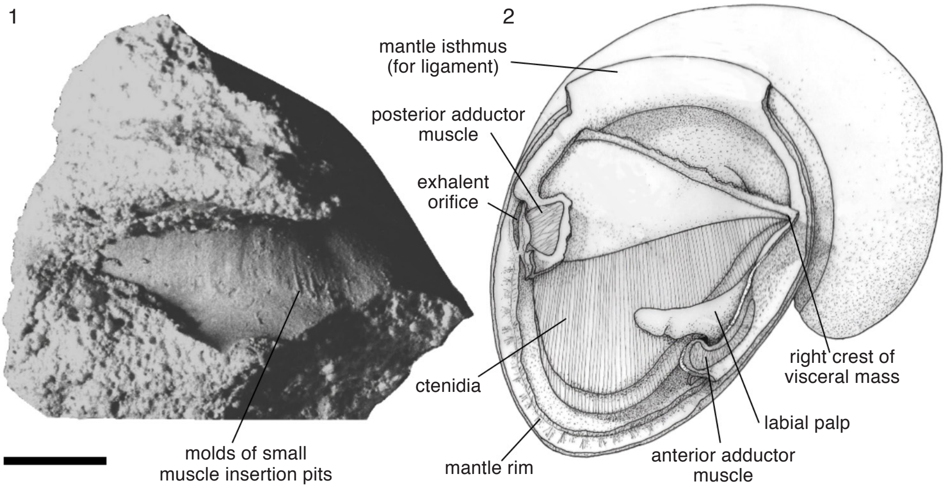

Fig.14. Anatomy of primitive rudists. *1,* Dorsal aspect of internal mold of left valve umbonal cavity of *Epidiceras perversum* (Sowerby, 1834) (Epidiceratidae), showing growth traces of small muscle insertion pits associated with dorso-lateral attachment of body to inner surface of valve, Oxfordian, Mortagne-au-Perche (Orne), France, scale bar, 5 mm (Skelton, 1978, fig. 6); *2,* reconstruction of anatomy of diceratids and epidiceratids, right side view with right valve and mantle lobe removed to reveal right side of body (adapted from Skelton, 1978, fig. 9e).

Nevertheless, many uncoiled rudist taxa, most notably the radiolitids and hippuritids, possess a distinct pair of radially oriented modifications of the postero-ventral valve walls variously generated by deviations or infoldings of the valve margins, each frequently associated with some kind of small commissural orifice (Fig. 16; see also Steuber, 1999b). Douvillé (1886) interpreted these paired structures as having been associated with mantle openings for inhalant (*respiratoire*) and exhalent (*anale*) currents, respectively, by reference to the locations of those openings in similar living suspension-feeding bivalves such as *Chama* Linnaeus, 1758. He instituted the convention widely used in the older rudist literature of labeling them E (*entrée*) and S (*sortie*). However, opinions have differed historically on exactly how the paired radial shell structures might have related to the postulated currents and also whether or not they were associated with siphons (e.g., Dechaseaux, 1947; Vogel, 1960; Chubb, 1971). Yet the likelihood, discussed above, that the mantle margins in these forms had taken over the function of food particle entrapment from the gills casts doubt on the legitimacy of such explicit interpretative labeling of the paired radial structures. Alternatively, they might, for example, have only been associated with anatomically separated sites of pseudofecal and fecal ejection (Skelton, 1976, 1979). Accordingly, there has been a preference in more recent rudist literature for using noncommittal descriptive labels

Fig. 13. Myophoral rotations in uncoiled rudists. *1a–c, Pachytraga paradoxa* (Pictet & Campiche, 1869) (Caprinidae), separated left valve (*a*) and right valve (*b*) of single articulated individual (*c*), with tips of teeth broken off in their respective sockets, facing direction of posterior myophore in each valve shown by *arrows,* NHM PI MB 129, Aptian, Rustrel (Vaucluse), France (Skelton, 2013a, fig. 13b, c, d, respectively) (see also Skelton & Masse, 1998); *2,* left valve of *Neokimbleia planata* (Conrad, 1855) (Caprinuloideidae), note facing direction of posterior myophore (*arrow* shows contrast with *1a*), USNMNH 547500, Albian, Texas, USA (Mitchell, 2013a, fig. 6E); *3,* postero-ventral radial section of articulated *Horiopleura lamberti* Douvillé, 1889 (Polyconitidae), showing complementary inclinations of posterior myophores and ectomyophoral cavity behind that of left (upper) valve, PWS, Albian, Santander, Spain; *am*, anterior myophore; *at*, anterior tooth (left valve); *ct*, central tooth (right valve); *ecto*, ectomyophoral cavity; *endo*, endomyophoral cavity; *lv*, left valve; *pm*, posterior myophore; *pt*, posterior tooth (left valve); *rv*, right valve; scale bars, 10 mm (new).

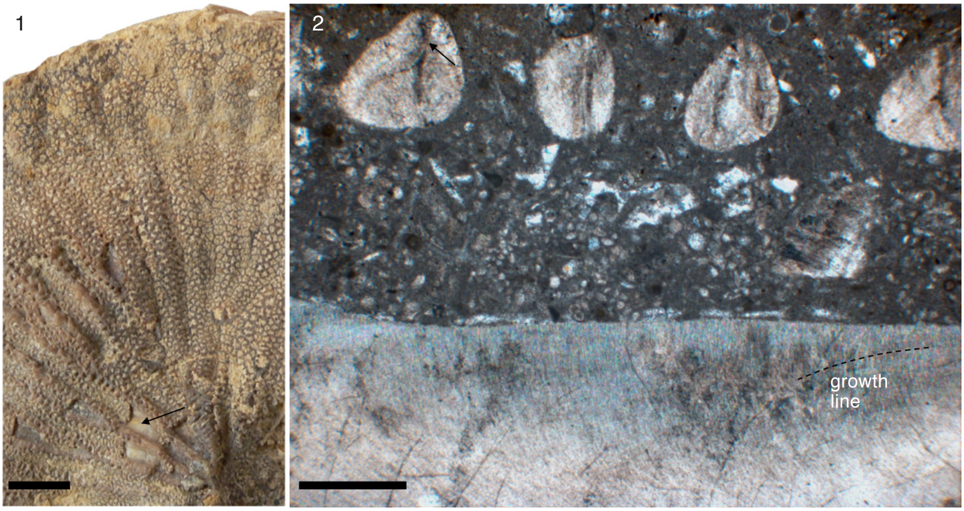

FIG. 15. Radial canal system of hippuritid rudists. *1,* detail of part of left valve of *Pseudovaccinites giganteus major* TOUCAS, 1904 (same specimen as Fig. 1.4), showing porous roofs of radial canals, partially eroded to reveal canals beneath (shown by *arrow*), PWS, scale bar, 10 mm (new); *2,* thin section photomicrograph in crossed-polarized light of radial section along canal in left valve outer shell layer of *Pseudovaccinites galloprovincialis* (MATHERON, 1843), Santonian, Riu Carreu valley, southern Central Pyrenees, Spain, valve margin to left of image, note how growth lines (perpendicular to fibrous prisms) line base of canal and wrap upwards around pore walls to meet at dark periostracal insertion lines on top (*arrow*), indicating original presence of mantle linings up canals to pore margins, PWS, scale bar, 0.5 mm (Skelton, 2013a, fig 9e)

for the paired structures instead, labels such as radial bands or pseudopillars (where infolded) for those seen in radiolitids, and pillars and oscules for those in hippuritids. (see Terms, p. 29–30).

An alternative interpretation of the trophic status of rudists, repeatedly postulated by a number of authors, is that of photosymbiosis, with the enlarged mantle margins presumed to have harbored photosynthesizing zooxanthellae. This hypothesis was arrived at by analogy with the living giant clam *Tridacna* BRUGUIÈRE, 1797 as well as with extant tropical hermatypic corals (e.g., PHILIP, 1972; COWEN, 1983; KAUFFMAN & JOHNSON, 1988; SEILACHER, 1998; VERMEIJ, 2013). The exceptionally large shell size attained by some (though by no means the majority of) rudists and their rapid proliferation on low-paleolatitude shallow marine carbonate substrates, sometimes in association with corals, might seem to lend the idea some plausibility. Nevertheless, the hypothesis remains essentially speculative, as it relies entirely upon circumstantial evidence that is merely consistent with it, but for which alternative explanations are available. Thus, for example, while shell size in most bivalves tends to be limited by decelerated adult growth following relatively rapid juvenile size increase, rudists were able to produce elongated tubular valves simply by maintaining juvenile-like, relatively high rates of incrementation over many years as adults (Fig. 17.1–17.2), similarly to the large Liassic bivalves of the *Lithiotis* GÜMBEL, 1871 facies (ACCORSI BENINI, 1985). Moreover, carbonate saturation in the exceptionally warm, shallow waters in which rudists thrived can, in any case, be expected to have favored high rates of calcification (SKELTON & GILI, 2012). Finally, it should be pointed out that the largest rudist shells invariably also economized massively on shell growth through the incorporation of various porous mesostructures such as pallial canals, cells, and/or tabulae (Fig. 10).

Additionally, some other arguments proposed for the photosymbiosis hypothesis turn out to be based on erroneous assumptions.

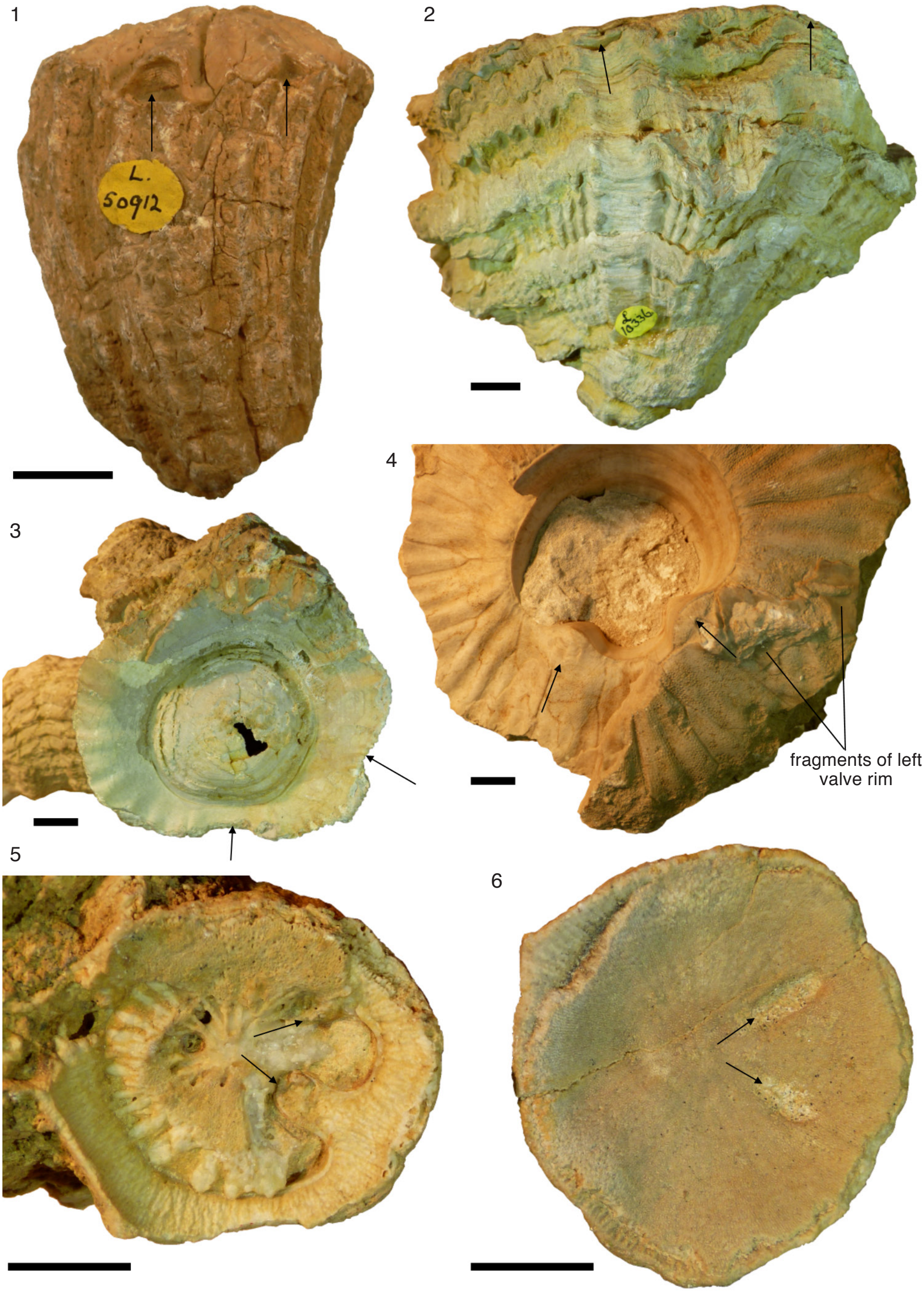

FIG. 16. Paired postero-ventral structures in rudist shells (indicated by *arrows*). *1,* Radial bands surmounted by orifices at valve margins in *Gorjanovicia endrissi* (BOEHM, 1927) (Radiolitidae), NHM L50912, Campanian, western Pontides, Turkey; *2,* smooth radial bands in *Radiolites mamillaris* MATHERON, 1843 (Radiolitidae), NHM L10336, Santonian, Mazaugues (Var), France; *3,* indentation of radial bands in *Durania cornupastoris* (DES MOULINS, 1826) (same specimen as Fig. 7.3); *4,* infolded pseudopillars in *Lapeirousia jouanneti* (DES MOULINS, 1826) (same specimen as Fig. 7.4); *5–6, Hippurites cornucopiae* DEFRANCE, 1821 (Hippuritidae), pillars in right valve (*5*), NHM LL41744, and corresponding oscules in overlying left valve (*6*), NHM LL41745, Maastrichtian, Jebel Faiyah, Sharjah, United Arab Emirates; scale bars: 10 mm (*1,* Fenerci-Masse, Skelton, & Masse, 2011, fig 12F; *2–6,* new).

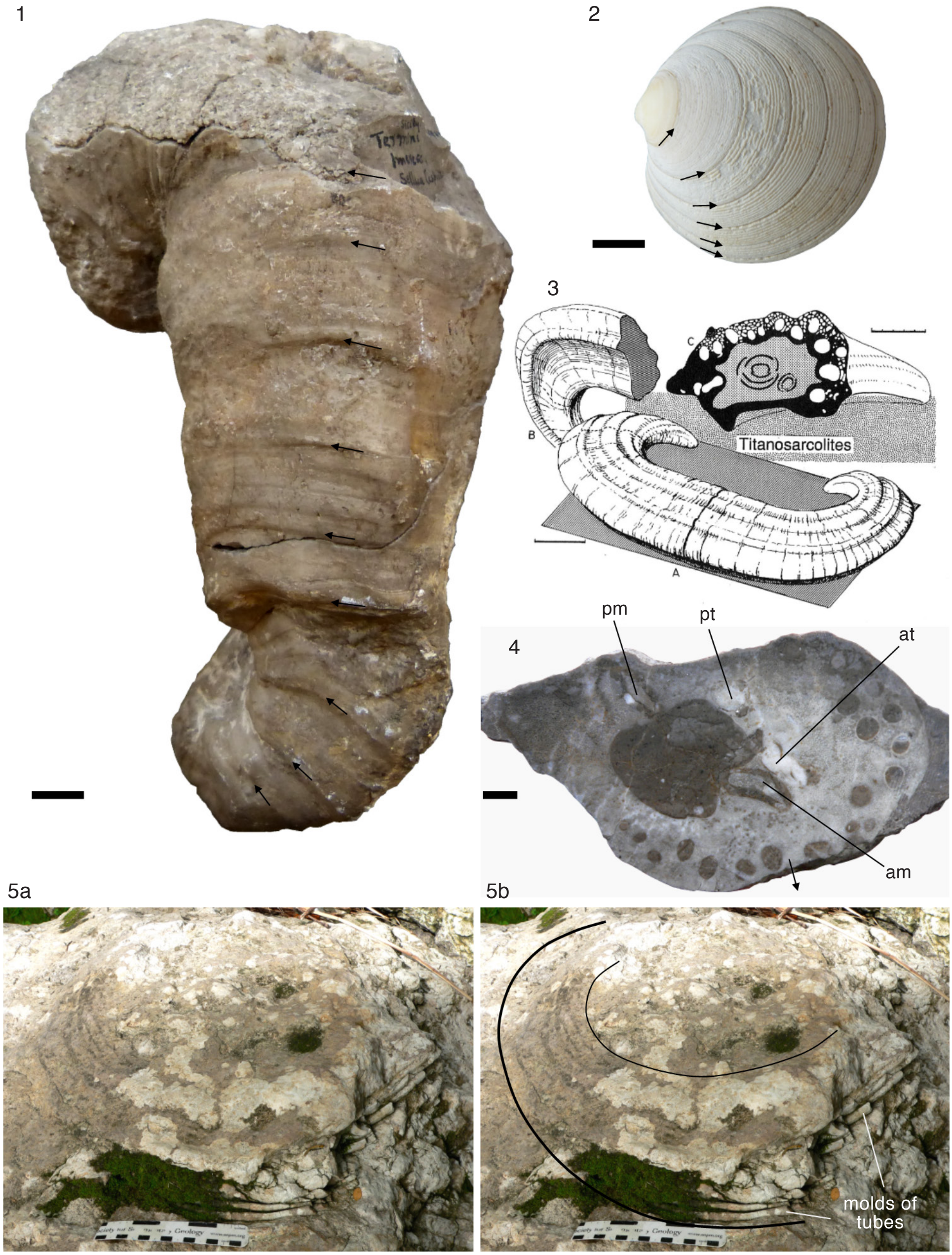

FIG. 17. Critique of supposed evidence for rudist photosymbiosis hypothesis (see p. 18–21 for discussion). *1,* Periodic, probably annual growth bands in *Sellaea cespitosa* DI STEFANO, 1889 (Caprinulidae), with *arrows* indicating sustained high growth rate from juvenile to adult shell, NHM (unregistered, but associated with L63120), Aptian, Termini Imerese, Sicily; *2,* extant *Dosinia exoleta* (LINNAEUS, 1758), showing successive narrowing of annual growth rings (*arrows*), hence marked slowing of growth rate in adult shell following rapid juvenile growth, PWS, northwest Wales, UK; *3,* life position of *Titanosarcolites* TRECHMANN, 1924 (Antillocaprinidae), with tubes on the upper surface as postulated by SEILACHER (Seilacher, 1998, fig. 9, reproduced with permission of publisher); *4,* transverse section through right valve (abumbonal view), with teeth and myophores inserted from left valve, of *Titanosarcolites giganteus* (WHITFIELD, 1897), *(Continued on facing page).*

For example, SEILACHER (1998) assumed that the large tubes in the giant recumbent form *Titanosarcolites* (TRECHMANN, 1924) (Fig. 1.7) were situated on the upper side of the shell in life (Fig. 17.3), apparently supporting his postulate that they were associated with zooxanthellate pallial diverticles. However, the usual mode of settlement on the substrate in rudists as well as shells that were actually preserved in life position consistently show the tubes to have been situated on the underside of the shell in life (Fig. 17.4–17.5a–b), thereby falsifying SEILACHER's speculation. The exceptional morphological modifications that allowed mantle exposure to light in the few rudist genera for which a case for photosymbiosis might be made, such as *Osculigera* KÜHN, 1933 (VOGEL, 1975) and *Torreites* PALMER, 1933 (SKELTON & WRIGHT, 1987) indeed set those taxa apart from other rudists. In contrast, the adaptation of pore-bearing hippuritids for filtering, as well as their occasional occupation of demonstrably non-oligotrophic environments, favor the parsimonious default interpretation that at least they (if not the great majority of rudists) were suspension feeders, just as are the majority of living bivalves (GILI, MASSE, & SKELTON, 1995).

Lastly, and very importantly, both the extraordinary morphological diversity of rudists and their contrasting distributions (e.g., MASSE & FENERCI-MASSE, 2008) imply considerable taxonomic variation in their life habits and environmental tolerances. Without the taxa involved being specified and supporting evidence cited, interpretations of the general significance of rudist associations in terms of such variables as nutrient flux, sedimentary context, and climatic conditions, should therefore be regarded as unreliable (SKELTON & GILI, 2012).

PHYLOGENY AND SYSTEMATICS

The classification of rudists adopted herein follows that of SKELTON (2013a, 2013b, itself a revision of that given in CARTER and others (2011) (Fig.18). This section links the classification of the group to its inferred evolutionary history. Most of the supra-generic taxa recognized are monophyletic, according to current phylogenetic analyses (e.g., SKELTON & MASSE, 1998; CHARTROUSSE, 1998b; SKELTON & SMITH, 2000; MASSE, 2002; SCOTT & others, 2010). When classifying fossil organisms according to the Linnaean system, however, novel grade-groupings and any available candidate ancestors (which appear as structural sister taxa on cladograms; CARTER & others, 2015) are necessarily assigned to different higher taxa of equivalent rank because the putative ancestors, by definition, lack the shared derived characters (synapomorphies) that diagnose the descendent groups—as in the analogous vertebrate case of birds and reptiles. In order to optimize the phylogenetic informativeness of the classification adopted here, paraphyletic families of candidate ancestral genera have been kept as small as current phylogenetic resolution allows, although scope certainly remains for further pruning with more probing phylogenetic analysis. Polyphyletic taxa, which misrepresent evolutionary relationships by pooling together taxa of independent ancestry, have been avoided, as far as present understanding allows.

The relative merits of alternative hypotheses for rudist ancestry have been little investigated since the detailed discussion of DECHASEAUX (1939), who concluded in favor of the derivation of *Diceras* LAMARCK,

FIG. 17. *(Continued from facing page).*
Campanian, Blue Mountain Inlier, Jamaica, note that the myocardinal elements (see MITCHELL, 2013c) confirm the downward-facing aspect of the tube-bearing anterior flank of the shell (*arrow*), which is characteristically applied to the substrate during the earliest growth stages in all rudists (Department of Geography and Geology Museum, The University of the West Indies, Mona Campus, Kingston, Jamaica); *5a–b, Titanosarcolites giganteus* preserved in life position (left valve outlined by *black lines* in *b*), showing tubes on the underside of the shell (contrary to *3*, but in agreement with *4*) Maastrichtian, Guinea Corn Formation, Central Inlier, Jamaica; *am,* anterior myophore; *at,* anterior tooth; *pm,* posterior myophore; *pt,* posterior tooth (all from left valve); scale bars: *1–2, 4,* 10 mm; *5a–b,* 13-cm-long ruler included for scale (*1–2, 4–5a–b,* new).

1805 (and *Epidiceras* Douvillé, 1936 by implication) ultimately from the Devonian *Megalodon* J. de C. Sowerby, 1827, via the Liassic *Protodiceras* Boehm, 1892. However, the remarkable stratigraphical gap between *Megalodon* and the variety of much later Triassic–Jurassic thick-shelled bivalves with pachyodont dentition suggests that these taxa may well be merely convergent with the much older *Megalodon*, *sensu stricto*. On the other hand, the Middle Jurassic megalodontiform bivalve *Pachyrisma* Morris & Lycett, 1850, for example, indeed shares all the essential features of the earliest rudists (spirogyrate umbos associated with a modified parivincular ligament, simple pachyodont dentition, and ledgelike posterior myophores), bar the presence of a fibrillar prismatic calcite outer shell layer, which has characterized rudists from their first appearance. Moreover, given that similar, but as yet undescribed, megalodontiform bivalves have been observed by the author in strata ranging up into the Lower Cretaceous, derivation of the first rudists from some such forms in the Oxfordian seems highly plausible; and accordingly, *Pachyrisma* was selected as an outgroup taxon for the cladistic analysis of rudists by Skelton and Smith (2000). Scope, nevertheless, remains for more critical investigation of rudist origins.

The cladistic analysis of Skelton and Smith (2000) revealed a fundamental phylogenetic dichotomy between rudists attaching by the left valve and those attaching by the right valve, confirming Douvillé's (1936) postulate of two evolutionary branches issuing from *Epidiceras* and *Diceras*, respectively. These two clades were formally established by Skelton (2013a, 2013b) as the suborders Requieniidina and Hippuritidina (Fig. 18). They should not be confused with the Dextrodonta and Sinistrodonta of Pchelintsev (1959), which, as their names indicate, are based instead upon dentition, the first group possessing Douvillé's (1886, 1887) normal dentition (see Internal Shell Features, page 9) and the second, his inverse dentition. Pchelintsev's (1959) suborders are thus separated at the transition between *Diceras* and *Valletia* Munier-Chalmas, 1873 within the Hippuritidina. Taxonomic division between the consequently paraphyletic Dextrodonta and monophyletic Sinistrodonta is rejected here in favor of the two purely monophyletic sister groups (Requieniidina and Hippuritidina) cited above.

A comprehensive classification of rudists was also proposed by Yanin (1990, 1995), in which a large number of new suprageneric taxa were introduced. However, many of the groupings recognized by him are polyphyletic according to the phylogenetic analyses followed here, while the numerous monogeneric subfamilies or even families of his scheme are phylogenetically uninformative. Moreover, his two suborders Diceratina Yanin, 1989 and Hippuritina Newell, 1965, although given taxon-based names, are exactly equivalent to Pchelintsev's (1959) two suborders, already rejected above.

THE REQUIENIIDINE CLADE

The diagnostic distinction between the monophyletic Requieniidae and the paraphyletic Epidiceratidae, from which the former emerged, arose from the evolution of more exaggerated asymmetry between the valves in the requieniids, such that the umbo of the attached left valve came to coil trochospirally to helicospirally across the commissural plane, thereby generating a broadly extended basal surface on the anterior wall of that valve (Gourrat, Masse, & Skelton, 2003) (see Fig. 1.2). Masse (2002) identified a subclade within the Early Cretaceous members of the Requieniidae consisting of *Requienia* Matheron, 1843, *Toucasia* Munier-Chalmas, 1873, and *Pseudotoucasia* Douvillé, 1911 that shared the derived development of relatively pronounced posterior myophores compared with their subdued state in *Matheronia* Munier-Chalmas, 1873 and *Lovetchenia* Masse, 1993. This basic distinction was supported by the cladistic analysis of Scott

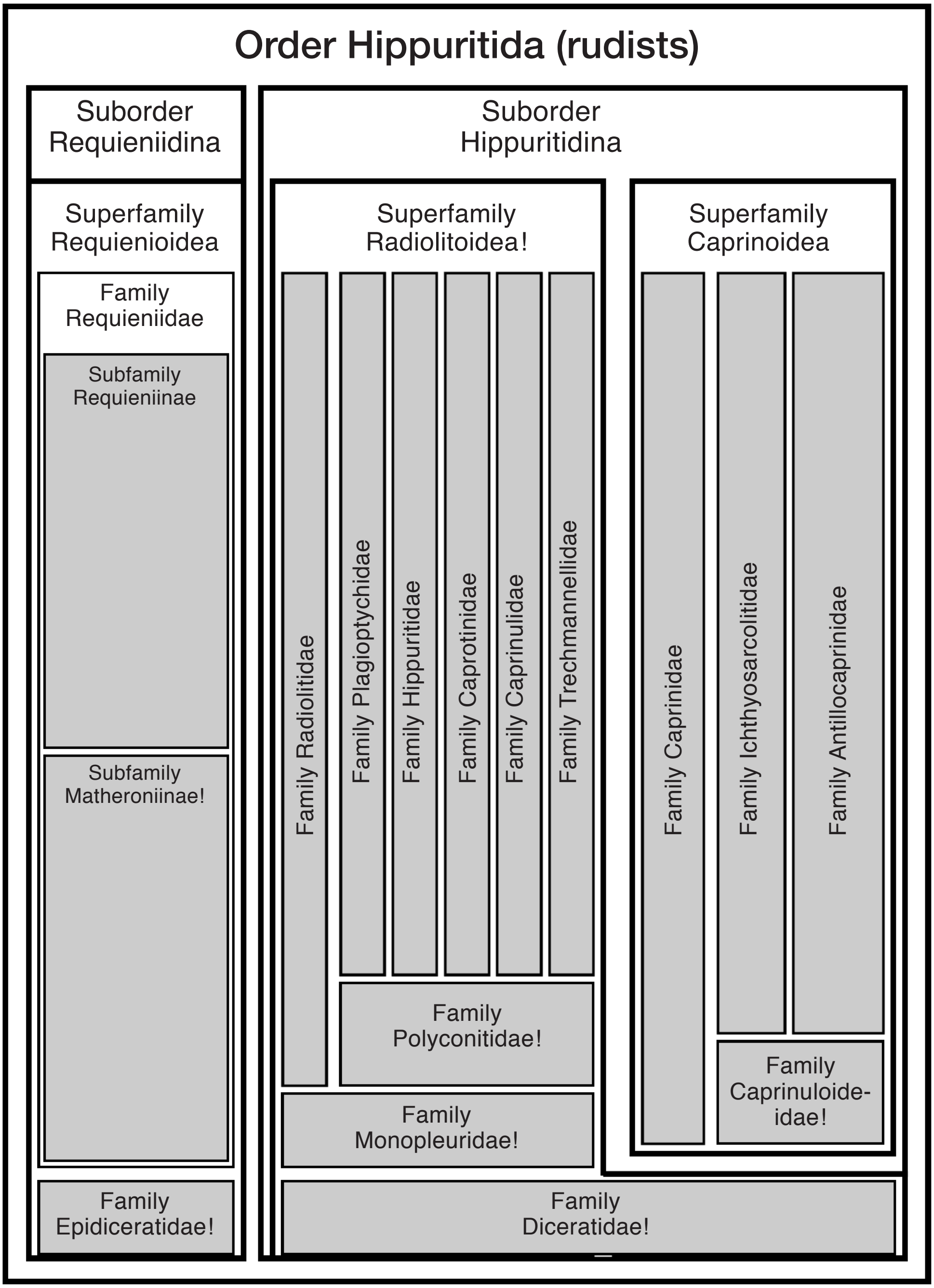

FIG. 18. Suprageneric classification of rudists used herein. Paraphyletic taxa are indicated by an exclamation point (!) and are considered to include the ancestors of the taxa stacked above them (Skelton, 2013a, 2013b). See pages 21–25 for discussion of phylogenetic basis (chart adapted from Skelton, 2013a, fig 1).

and others (2010), who established two subfamilies for the two groupings (including other genera).

THE HIPPURITIDINE CLADE

Two distinct clades of uncoiled rudists emerged from the paraphyletic Diceratidae, the first comprising the superfamily Caprinoidea (as currently recognized and described below), and the second, all the remaining uncoiled rudists. The stem-group diceratids are combined, for nomenclatural economy, with the second (unnamed) clade in the present classification to constitute the superfamily Radiolitoidea (Fig. 18), which is thus minimally paraphyletic. At present, it is not clear whether the two uncoiled clades are sister taxa that evolved from a common ancestor in which ligamentary invagination was already present (see External Shell Form and Ligament, p. 1), or whether they arose from different diceratid lineages in which ligamentary invagination evolved independently. Resolution of this question will require further detailed investigation of Late Jurassic to earliest Cretaceous rudist taxa. Either way, the earliest caprinoideans and uncoiled radiolitoideans are distinguished from each other on the basis of dentition. The caprinoideans retain relatively primitive inverse dentition, with the posterior tooth distinctly smaller than the anterior tooth (e.g., Fig. 13.1a) in a more or less umbonally extended left valve, similarly to the diceratid *Valletia* (Fig. 11.3a–b). The uncoiled radiolitoideans, meanwhile, immediately began to approach the derived conditions of more equal teeth and a low capuloid to gently domed left valve (e.g., Fig. 11.4).

Skelton (1978) and Skelton and Smith (2000) criticized the polyphyletic composition of the families Caprinidae (based only on shared possession of pallial canals) and Caprotinidae (likewise for accessory cavities) as conceived in the former *Treatise* classification by Dechaseaux and others (1969). Included in the Caprinidae by Dechaseaux and others (1969) were a number of canaliculate groups, the likely independent origins of which had been cogently advocated many years earlier by Douvillé (1887, 1888, 1889) and Mac Gillavry (1937). Accordingly, three such groups were removed from the Caprinidae (*sensu* Dechaseaux & others, 1969) by Skelton (1978) to form distinct families (Ichthyosarcolitidae Douvillé, 1887; Antillocaprinidae Mac Gillavry, 1937; and Plagioptychidae Douvillé, 1888), though without supporting cladistic analysis at that time. Subsequently, the family Dictyoptychidae Skelton (in Skelton & Benton, 1993; =Trechmannellidae Cox, 1934 in the current classification) was also separated off. A further depletion of the former *Treatise* (1969) caprinid constituency followed the demonstration by Steuber and Bachmann (2002) that *Neocaprina* Pleničar, 1961 and *Caprinula* d'Orbigny, 1847 were probably derived from the radiolitoidean rudist genus *Sellaea*, a conclusion later confirmed by cladistic analysis (Sano & others, 2014). This grouping of genera was thus recognized by Skelton (2013a) as a distinct radiolitoidean family, Caprinulidae Yanin, 1990 (Fig. 18).

The remaining former *Treatise* (1969) caprinids are united by the presence of a large posterior endomyophoral cavity in the left valve (Fig. 13.1a–13.2; see Terms, p, 29), but they have been further divided by cladistic analysis into two subclades (Chartrousse, 1998a, 1998b; Skelton & Masse, 1998; Skelton & Smith, 2000) and are now established as the families Caprinidae d'Orbigny, 1847, and Caprinuloideidae Damestoy, 1971, within the Superfamily Caprinoidea d'Orbigny, 1847 (Skelton, 2013a; Fig. 18). The diagnostic basis for this distinction between the two families is the contrast in the sense of rotation of the posterior adductor from the commissural plane (Fig. 13.1–13.2; see Internal Shell Features, p. 9). Further subdivision of the Caprinuloideidae into constituent subfamilies was undertaken by Mitchell (2013a).

Further studies of New World canaliculate rudists have since phylogenetically reconnected two of the families that were separated by Skelton (1978) with the Caprinuloideidae, thus rendering the family paraphyletic (Fig. 18). Following the recognition by Aguilar-Pérez (2008) of a species of *Ichthyosarcolites* Desmarest, 1812 in Mexico, a genus previously regarded as limited to the Old World, Mitchell (2013b) proposed a caprinuloideid ancestry for the Ichthyosarcolitidae. Additionally, a cladistic study of antillocaprinids by Mitchell (2013c) identified a caprinuloideid ancestry for them as well. On the other hand, the proposal of polyconitid ancestry for the Plagioptychidae by Skelton and Smith (2000) has received support from the discovery of a canaliculate polyconitid, named *Magallanesia* Sano & others, 2014, in the western Pacific region (Sano & others, 2014). Among other Late Cretaceous canaliculate taxa, the origin of the Trechmannellidae (=Dictyoptychidae) remains obscure; on the other hand, the attribution of *Pseudosabinia* Morris & Skelton, 1995 to the Radiolitidae d'Orbigny, 1847, is now well established (Özer, 2010a; Korbar & others, 2010). The case for *Sabinia* Parona, 1908 being a radiolitid also remains plausible, following Philip (1986) and Morris and Skelton (1995).

For the polyphyletic Caprotinidae of Dechaseaux and others (1969), Skelton (1978) adopted a different approach, combining them with the basal Monopleuridae Munier-Chalmas, 1873 (under the first family name) so as to create a single broad rootstock for other, more derived clades of uncoiled rudists. However, such large paraphyletic stem groups obscure basal relationships (Smith, 1994), which the cladistic analysis of Skelton and Smith (2000) thus set out to resolve. One phylogenetic subgrouping accordingly confirmed was the family Polyconitidae Mac Gillavry, 1937, characterized by shared possession of a reflexed platelike posterior myophore in the left valve, separated from the posterior valve margin by a pronounced ectomyophoral cavity (e.g., Fig. 13.3). Though ignored by Dechaseaux and others (1969), Mac Gillavry's phylogenetic grouping was reaffirmed by Masse (1996) and Masse, Arias, and Vilas (1998), while the analysis of Skelton and Smith (2000) further identified it as a stem group for several other rudist families, including, notably, the Hippuritidae, which are characterized by a pair of infolded pillars in the right valve with matching oscules in the left valve (Fig. 16.5–16.6), and the canaliculate Plagioptychidae (Fig. 18).

Following Skelton (2013a), the family Caprotinidae, *sensu stricto*, is now provisionally limited to just two closely related genera, *Caprotina* (d'Orbigny, 1850) and *Chaperia* Munier-Chalmas, 1873 because of their currently uncertain phylogenetic position. Derivation from either a monopleurid (e.g., *Gyropleura* Douvillé, 1887), or a polyconitid (e.g., *Praecaprotina* Yabe & Nagao, 1926) seem equally possible. The family Monopleuridae, meanwhile, is recognized as a much-reduced basal group of uncoiled radiolitoidean rudists (Fig. 18) with a low capuloid to operculiform left valve bearing two subequal to equal teeth and simple myophores extending ventrally from the hinge plates, oriented either parallel to the commissural plane (e.g., Fig. 11.4) or with one or both of the left valve myophores tilted down into the right valve so as to face outwards onto their depressed counterparts there (Masse & Fenerci-Masse, 2009). Besides the Polyconitidae, the Monopleuridae appear to have also given rise to the largest rudist family, the Radiolitidae d'Orbigny, 1847 (Fig. 18), characterized by a projecting crescentic myocardinal arc in the left valve with subequal, pronglike teeth and platelike myophores, both of which face outwards onto the inner wall of the right valve (e.g., Fig. 11.5, Fig. 12.5).

PALEOBIOGEOGRAPHICAL DIMENSIONS OF RUDIST EVOLUTION

Although the earliest rudists known (diceratids and epidiceratids) come from Oxfordian successions in the northern

Tethyan margin of Europe (Karczewski, 1969), the Tithonian record already testifies to a few cosmopolitan genera ranging from Nova Scotia to Japan, with representatives in both northern and southern Tethyan regions (Sano & Skelton, 2010; Skelton, Sano, & Masse, 2013) (Fig. 19.1). Hence, given the limited number of studies upon which this record is based, it would be premature to attempt to locate exactly where within the Tethyan Realm the rudists originated.

The first clear evidence of rudist provincialism along the low-latitude Atlantic-Tethyan oceanic belt is seen in Hauterivian strata, with the disjunct appearance of the first representatives of the caprinoid sister taxa Caprinuloideidae and Caprinidae (Fig. 18) in the Caribbean region and in the Tethyan region, respectively (Skelton & Masse, 1998; Skelton, Sano, & Masse, 2013). Nevertheless, by Barremian times, members of the Caprinidae had possibly already spread as far east as Japan (Sano & others, 2012), as well as westwards to the Caribbean Province (Chartrousse & Masse, 1998; Pantoja-Alor, Skelton, & Masse, 2004), where they accompanied diverse caprinuloideids through the Early Aptian phase of expansive carbonate platform growth (Alencáster & Pantoja-Alor, 1996, 1998; Chartrousse & Masse, 2004; Scott & Hinote, 2007). The first direct evidence for rudist colonization of Pacific seamounts comes from core samples of Barremian (or possibly Hauterivian) age (Swinburne & Masse, 1995), immediately followed in the Early Aptian by the spread of Caribbean-derived caprinuloideids across the Pacific to Japan (Skelton, Sano, & Masse, 2013; Fig. 19.2). Also in the Barremian to Early Aptian, some north-south differentiation was expressed in the Mediterranean Tethyan region, mostly at species level and again most clearly among caprinids, although also by some other endemic rudist taxa, such as the central and southern Tethyan *Glossomyophorus* Masse, Skelton, & Slisković, 1984 (see also Masse, 1992; Masse & others, 2015). However, in this region, the distributional record was blurred by some striking, probably climatically influenced latitudinal shifts (Masse & Fenerci-Masse, 2008).

Following a mass extinction of rudists in the mid-Aptian (Steuber & others, 2016; see *Treatise Online,* Part N, Chapter 26C), the caprinoids temporarily disappeared from the known stratigraphical record to some as yet unknown (possibly Pacific) refuge, in concert with a phase of global climatic cooling (Skelton & Gili, 2012). The caprinuloideids subsequently made a Lazarus-style reappearance in the Caribbean Province at the end of the Aptian and rapidly diversified alongside other rudists, including some endemic species, on Albian carbonate platforms there (Scott & Filkorn, 2007). Meanwhile, the Late Aptian–Albian also witnessed a rapid spread of rudists, especially radiolitids and polyconitids, both with a thickened calcitic outer shell layer, along the Tethyan platforms, including some new endemic genera characterizing a distinct southwest Asian/western Pacific rudist faunal province (Masse & Gallo-Maresca, 1997; Sano & Masse, 2013; Skelton, Sano, & Masse, 2013; Rao & others, 2015). During that same time interval, the equatorial Pacific played an important role in rudist evolution, with contrasting pathways of dispersion, possibly including the reintroduction of *Caprina* d'Orbigny, 1822 into the Tethyan region in the Late Albian (Skelton, Sano, & Masse, 2013; Fig. 19.3), as well as extending the range of the newly evolved ichthyosarcolitids from the Caribbean Province to the Old World in the Albian (Mitchell, 2013b; Steuber & Bachmann, 2002). By contrast, the stepwise demise of Japanese platforms and rudists in the latest Aptian/early Albian marked the separation from the Tethyan Biotic Realm of a distinct "North Pacific Biotic Province," probably as a result of changes in oceanic circulation (Iba & Sano, 2007).

A radical change of rudist paleobiogeography ensued in the Cenomanian with the apparent demise and drowning of Pacific platforms and severe reduction of Caribbean ones, leaving only a few exceptions such as the Morelos Platform in southwest Mexico, hosting undetermined caprinids—as they were termed by Aguilera-Franco and Allison (2004)—most likely caprinuloideids in the revised classification used herein. Otherwise, a diagnosed caprinuloideid has also been recorded (as a probably dried-out and floated shell) from the Middle Cenomanian of Montana (Mitchell, 2013d). In the Old World Tethys, by contrast, there was massive expansion of carbonate platforms in the Cenomanian. These platforms hosted abundant radiolitids (e.g., Fig. 2) and, especially along the platform margins, diverse canaliculate rudists of largely aragonitic shell composition—owing to extreme thinning of their calcitic outer shell layer—comprising caprinids, ichthyosarcolitids, and caprinulids. Such associations extended from the Mediterranean Tethyan region in the west (Philip, 1981; Steuber & Löser, 2000) as far east as the Tarim Basin (Lan & Wei, 1995), and southwards to southeast Arabia (Philip, Borgomano, & Al-Maskiry, 1995).

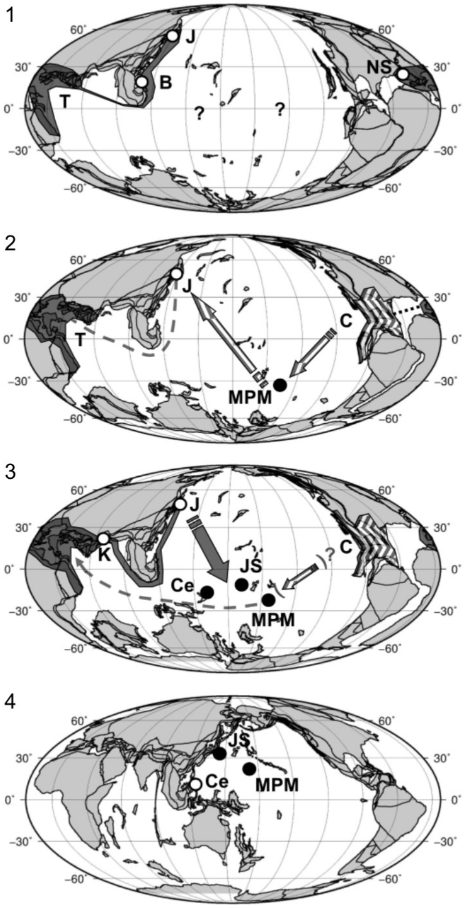

Fig. 19. Palaeogeographical maps centered on the Pacific Ocean illustrating its role in the evolution and distribution of rudists for four time intervals. *1,* Tithonian–Berriasian (map for 145 Ma); *2,* Barremian–Early Aptian (map for 120 Ma); *3,* Late Aptian–Albian (map for 100 Ma); *4,* present-day map to show current positions of drifted Pacific oceanic localities. Abbreviations: *B,* Borneo; *C,* Caribbean Province (*cross-hatched pattern*), with Pacific range extension in *2* and *3; Ce,* Central Cebu, Philippines; *J,* Japan; *JS,* Japanese Seamounts; *K,* Kohistan (northern Pakistan); *MPM,* Mid-Pacific Mountains; *NS,* Nova Scotia; *T,* Tethyan Province (*dark gray shading*), with Pacific range extension in *1–3*. Maps, using Mollweide projection, generated from ODSN Plate Tectonic Reconstruction Service (Hay & others, 1999) (adapted from Skelton, Sano, & Masse, 2013).

Another mass extinction at the end of the Cenomanian led to a major turnover of rudist families, most notably including the final extinction of the caprinids and ichthyosarcolitids (Philip & Airaud-Crumière, 1991) and maybe also the caprinulids, with the one possible exception of the late Campanian–Maastrichtian *Pseudocaprinula* Bilotte, 2015 in the Pyrenees. The surviving radiolitids, on the other hand, rapidly rediversified along the entire Tethyan Realm (Philip, 1998; Steuber & Löser, 2000). The first hippuritids appeared at about the same time in the early Turonian of both the New World (Aguilera-Franco & Allison, 2004) and the Old World, from Western Europe to Arabia (Philip, 1998). The massive production of bioclasts from the abundantly clustered shells of these last two families, both characterized by a thickened calcitic outer shell layer (e.g., Fig. 4, Fig. 7.3–7.6), coupled with the loss of the largely aragonitic canaliculate taxa of the Cenomanian, significantly modified the petrological composition of platform bioclastic deposits. This change had feedback effects not only on the diagenesis of these deposits and their susceptibility to current reworking (Carannante & others, 1999; Simone & others, 2003), but also on seawater chemistry, including, for example, its strontium/calcium ratio (Steuber, 2002).

During this last major phase of rudist evolution, from the Turonian to their final extinction at the close of the Maastrichtian, rudists reached their maximum taxonomic diversity (as well as paleolatitudinal spread) in the Late Campanian (see Steuber & others, 2016; *Treatise Online,* Part N, Chapter 26C). Changes in paleogeography contributed to this diversification by enhancing provinciality. Thus, besides allowing the vicariant differentiation of radiolitids, hippuritids, and plagioptychids at species and even generic level, the widening Atlantic barrier between the New World and the Old World confined the diversification of the caprinuloideid-derived family Antillocaprinidae (Mitchell, 2013c) to the New World, alongside some likewise endemic lineages of multiple-fold hippuritids (Mitchell, 2010). Meanwhile, the kaleidoscopic geodynamic choreography of carbonate shelves and platforms in and around the Tethyan Ocean, produced by the oblique, jawlike convergence of its northern and southern margins, yielded a more blurred pattern of regional differentiation. The clearest distinction arose between the northwest Tethyan margin (France and Iberia) and the remaining Mediterranean Tethyan regions, largely through the accumulation of new taxa in the latter (Philip, 1998; Steuber & Löser, 2000), amongst which a number of distinctive radiolitid genera were especially prominent (Sladić-Trifunović, 1989). Farther east, the southeast Tethyan flank of the African/Arabian plate additionally hosted a number of distinctive endemic rudist taxa, most notably the trechmannellids, besides numerous taxa shared with the Mediterranean Tethyan regions (Morris & Skelton, 1995; Steuber & others, 2009; Khazaei, Skelton, & Yazdi, 2010; Özer, 2010b). Nevertheless, the Campanian–Maastrichtian interval also witnessed a limited resurgence of trans-Pacific range extensions (Skelton, 1988; Philip, 1998).

As discussed in Steuber and others, 2016 (see *Treatise Online,* Part N, Chapter 26C), the final, catastrophic extinction of the rudists is attributed to the effects of the terminal Cretaceous impact event upon the widespread but by then increasingly provincially isolated rudist associations of the Maastrichtian. The possible roles of Late Campanian–Maastrichtian cooling, overall sea-level fall, and associated changes in ocean circulation (Gale, 2000) in Maastrichtian distributional changes, though likely, nevertheless remain unclear in detail and require further investigation.

TERMS USED IN THE DESCRIPTION OF RUDIST MORPHOLOGY

Abapical/abumbonal. Orientational term applied to a transverse section of a valve viewed as if looking from the apical, or umbonal end of the valve towards its commissural end. When a right valve is viewed thus, with its dorsal margin at the top, anterior is to the right and posterior to the left (e.g., Fig. 10.1), and the converse is so for a left valve.

Accessory cavity. Discrete cavity that opens into the interior of a rudist valve, other than a tooth socket, and which is more or less separate from the main body cavity. An accessory cavity that lies on the outer side of a myophore (thereby separating it from the valve wall) is termed an ectomyophoral cavity (e.g., Fig. 13.3), while one that is situated directly to the inside of a myophore and is separated from the body cavity by a lamina is termed an endomyophoral cavity (e.g., Fig. 13.1a).

Adapical/adumbonal. Orientational term applied to a transverse section of a valve, meaning viewed as if looking from its commissural end towards the apex, or umbo of the valve (equivalent to looking into an isolated valve). When a right valve is viewed thus, with its dorsal margin at the top, anterior is to the left and posterior to the right (e.g., Fig. 3.4a), and the converse is so for a left valve.

Anterior myophore. See myophore.

Anterior tooth. See dentition.

Arête cardinale. See ligament.

Capuloid. Used in reference to the shape of an upper valve: cap-shaped with the umbo usually projecting obtusely in the style of a Phrygian (or French Liberty) cap (e.g., Fig. 1.6, Fig. 13.1c).

Celluloprismatic mesostructure. Distinctive modification of the calcitic outer shell layer in the right valve and, in some, also the left valve of most (but not all) radiolitids, consisting of repeatedly stacked layers of tiny (usually of millimetric, to submillimetric width) hollow cells (Fig. 7.4–7.5). In each cell layer, the bounding vertical walls of the cells were built up from a continuous basal surface by localized enhancement of incremental shell growth and abruptly capped off by the floor of the succeeding cell layer, on which the cell growth process was repeated (Regidor-Higuera, García-Garmilla, & Skelton, 2007).

Central tooth. See dentition.

Dentition. The arrangement of the interlocking hinge teeth and sockets forming part of the aragonitic inner shell in rudists, with two prominent, knobby, pachyodont teeth (anterior and posterior) in one valve situated on either side of one (central) tooth in the other. Primitive normal dentition consists of two teeth in the right valve and one, plus an incipient posterior toothlet, in the left valve (Fig. 11.1–11.2), while derived inverse dentition comprises two left valve teeth and one right valve tooth (Douvillé, 1887; 1896) (Fig. 3.3a–3.4a, 11.3–11.4). The central tooth is reduced or even lost in some highly derived inverse forms (Fig. 11.5), while others possess supplementary toothlets (e.g., some antillocaprinids; Mitchell, 2013c).

Ectomyophoral cavity. See accessory cavity.

Endomyophoral cavity. See accessory cavity.

Left valve. See shell.

Ligament. Primitively, rudist shell valves were connected by a functional external dorsal ligament of modified parivincular type (i.e., of C-shaped cross section, with an extensional outer lamellar layer inserting along a flat, tracklike bourrelet and a compressive inner fibrous layer attached to the outer face of a thickened nymph in each valve; Fig. 3.1). In the majority of rudists attaching by the right valve, however, the ligament was secondarily invaginated (Fig. 3.3–3.4; see also Skelton, 1978, 1979), so becoming ineffective, and was eventually lost in some more derived forms. In some taxa, most notably in radiolitids, hippuritids, and some caprinoids, it became drawn inwards at the tip of an acute infolding of the outer shell layer (e.g., Fig. 3.4a–b, Fig. 7.6), sometimes referred to in the literature as the *arête cardinale*.

Myophore. Projection or sloping buttress on the inside of the shell supporting the insertion of an adductor muscle (e.g., Fig. 12.4–12.5 and Fig. 13). All rudists possessed myophores as part of the aragonitic inner shell (Fig. 8), displaying a taxonomically useful variety of forms, and in some cases, tilted in such a way as to yield neighboring accessory cavities (e.g., Fig. 13).

Myocardinal apparatus. The combined dentition and myophores, which in most rudist taxa are closely associated in each valve (e.g., Fig. 11.3–11.5, Fig. 13.1–13.2). The configuration of the myocardinal apparatus is of fundamental importance in the higher-level taxonomy of rudists.

Oscules. External openings in the hippuritid left valve formed by infolding of the valve margin above the heads of the pillars (Fig. 16.5–16.6). Similar structures are also present in the left valve of a few derived radiolitids.

Outer shell layer. See shell.

Pallial canals. Elongate, blind-ending canals penetrating the shell from the inner surface of one (usually the upper) or both valves, which in life housed papillae projecting from the outer surface of the mantle (Vogel, 1978; Fig. 10.1–10.2). In many taxa their openings are limited to the periphery of the inner (aragonitic) shell, where they usually show a radially oriented, narrow tearlike to flamelike (pyriform), or subrectangular cross-sectional shape. In more derived taxa, canals of polygonal or rounded cross-sectional shape may invade the inner parts of the valve as well, eventually even including the teeth and/or myophores in some (e.g., Fig. 10.1). Pallial canals vary considerably in size and shape in different taxa and may contain tabulae in some. The term pseudocanals is sometimes used in the literature for those found in the inner shell of certain derived radiolitids (e.g., *Colveraia* Klinghardt, 1921). Although those in *Colveraia,* for example, evolved independently from the canals seen in caprinids, (i.e., they are not homologous), they are nevertheless basically analogous in terms of mode of formation. Use of the term pseudocanal dates from when virtually all canaliculate rudists other than the radiolitid examples were systematically treated as if they were related (as caprinids *sensu lato*; e.g., in Dechaseaux & others, 1969). But with the explicit recognition that canals evolved independently in several different clades (as reflected in the classification herein), the distinction between canals and pseudocanals has become meaningless, rendering the latter term redundant. Exceptionally, in a few radiolitids (e.g., *Joufia* Boehm, 1897), radiating canals also evolved in the calcitic outer shell layer of the left valve (Fig. 1.5). Vogel (1978) discussed a variety of possible (and not mutually exclusive) functions for pallial canals—from weight reduction and economic provision of shell rigidity as well as inhibition of penetration by boring organisms to enhancement of respiration and/or suspension feeding on the expanded mantle surface. Indeed, given the variety of form and distribution of canals among different groups of rudists, it is likely that any functions associated with them were correspondingly diverse. However, the pore and canal system in the outer shell layer of the left valve in hippuritids (Fig. 7.6, Fig. 15) is fundamentally distinct from the internally closed pallial canals, as they retain links with the outside via the open pores, through which they probably conducted suspension-feeding currents (Skelton, 1976; Schumann, 2010).

Parivincular ligament. See ligament.

Pillars. A pair of radial infoldings of the outer shell layer on the posterior flank of the right valve in hippuritids (Fig. 16.5); oscules are formed by the corresponding infoldings in the operculiform left valve (Fig. 16.6).

Posterior myophore. See myophore.

Posterior tooth. See dentition.

Radial. Term applied to any feature (e.g., ribs, costae, or pallial canals) or plane of section (e.g., Fig. 8.1a), with an umbo-to-commissure orientation (or one that bisects any conical rudist valve perpendicularly to the commissural plane).

Radial bands. A pair of radially oriented, discretely demarcated bands on the posteroventral flank of the attached valve of certain rudist taxa, each usually associated with some kind of small commissural orifice, most notably the radiolitids, in which their morphology is of taxonomic importance (Fig. 7.3, Fig. 16.1–16.3).

Right valve. See shell.

Shell. Rudist bivalves are inequivalve, with one valve—either the left valve or the right valve, according to taxon—attached at least initially to some hard surface, and the other remaining free. All have an outer shell layer of variable thickness (Fig. 7), consisting of fibrous low-Mg calcite (Fig. 4), and an originally aragonitic (though rarely preserved thus) inner shell, which includes the teeth and myophores (Fig. 8). Primitively, the outer shell layer is relatively thin (~1 mm; e.g., Fig. 1.1, Fig. 7.1), but secondary thickening is a diagnostic character for certain taxa (e.g., Fig. 7.2–7.6).

Spirogyrate growth. Spiral valve growth in the style of a ram's horn, due to continuous tangential displacement of successive shell growth increments, causing the umbos to twist around as they are built out from the commissural margin (Fig. 1.1–1.2). Forward-spiraling umbonal growth is termed prosogyrate (Fig. 3.1), and backward-spiraling (a secondary condition in some uncoiled rudists) is termed opisthogyrate.

Tabulae. Partitions serving as false floors within the body cavity, and/or other cavities in the inner shell of some rudists (e.g., Fig. 9.1a–b, Fig. 10.2–10.3).

Transverse section. Section cutting across any conical rudist valve more or less parallel with the commissural plane—hence, perpendicular to a radial section (e.g., Fig. 10.1). Note that this definition differs from that used in an anatomical sense for equivalved bivalves, in which a transverse section cuts across both valves, perpendicular to the commissural plane.

Uncoiled growth. Tubular (conical to cylindrical) valve growth (e.g., Fig. 1.3–1.7) permitted by removal of the constraint of continuous tangential displacement of successive shell growth increments associated with invagination of the ligament in rudists (in contrast to spirogyrate growth).

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ABBREVIATIONS FOR MUSEUM REPOSITORIES

NHM: The Natural History Museum, London, UK
USNMNH: United States National Museum of Natural History, Smithsonian Institution, Washington, DC, USA
PWS: Peter W. Skelton personal collection, Milton Keynes, UK
XZG: Nanjing Institute of Geology and Palaeontology, Chinese Academy of Sciences, Nanjing, China

REFERENCES

Accorsi Benini, Claudia. 1985. The large Liassic bivalves: Symbiosis or longevity. Palaeogeography, Palaeoclimatology, Palaeoecology 52:21–33.

Aguilar Pérez, Javier. 2008. Rudistas del Cretácico Inferior y Medio, Barremiano?–Cenomaniano, Noreste y Centro de México. Ph.D. thesis, Universitat Autònoma de Barcelona. 139 p.

Aguilera-Franco, Noemí, & Peter Allison. 2004. Events of the Cenomanian-Turonian succession, southern Mexico. Journal of Iberian Geology 31:25–50.

Alencáster, Gloria, & Jerjes Pantoja-Alor. 1996. New Early Aptian Rudists (Bivalvia-Hippuritacea) from the Huetamo Area in Southwestern Mexico. Revista Mexicana de Ciencias Geológicas 12 (for 1995):123–134, 4 pl.

Alencáster, Gloria, & Jerjes Pantoja-Alor. 1998. Two New Lower Cretaceous Rudists (Bivalvia-Hippuritacea) from the Huetamo Region; Southwestern Mexico. Geobios Mémoire Spécial 22:15–28.

Astre, Gaston. 1930. Sur un *Agria* du Liban. Compte rendus de l'Association française pour l'Avancement des Sciences, Sciences naturelles. Géologie et Minéralogie 3:149–151.

Astre, Gaston. 1961. *Pachytraga* tubuleux du Barrémien du Doubs. Société d'Histoire Naturelle de Toulouse, Bulletin 96:205–222.

Bilotte, Michel. 2015. Révision de *Caprina incerta* Leymerie, 1878, rudiste du Crétacé supérieur pyrénéen et attribution au nouveau genre *Pseudocaprinula*. Annales de Paléontologie 101:119–126.

Boehm, Georg. 1892. *Megalodon, Pachyerisma* und *Diceras*. Berichte der Naturforschenden Gesellschaft zu Freiburg-i-Breisgau 6:33–56.

Boehm, Georg. 1897. Beitrag zur Gliederung der Kreide in den Venetianer Alpen. Zeitschrift der deutschen geologischen Gesellschaft 49:160–181.

Boehm, Johannes 1927. Beitrag zur Kenntnis der Senon fauna der Bithynischen Halbinsel. Paleontographica 69:187–222.

Bruguière, Jean G. 1797. *In* J. G. Bruguière, J.-B. de Lamarck & J. B. G. M. Bory de Saint-Vincent. Vers, coquilles, mollusques, et polypiers. *In* J. G. Bruguière, J.-B. de Lamarck, J. B. G. M. Bory de Saint-Vincent, G. P. Deshayes, & O. F. Müller, 1791–1827. Tableau Encyclopédique et Méthodique des Trois Règnes de la Nature Contenant L'Helminthologie, ou les Vers Infusoires, les Vers Intestins, les Vers Mollusques ... Vol. 2. H. Agasse. Paris. pl. 235.

Carannante, Gabriele, Roberto Graziano, Gerardo Pappone, Daniela Ruberti, & Lucia Simone. 1999. Depositional system and response to sea level oscillations of the Senonian rudist-bearing carbonate shelves. Examples from Central Mediterranean areas. Facies 40:1–24.

Carter, Joseph G., C. R. Altaba, L. C. Anderson, Rafael Araujo, A. S. Biakov, A. E. Bogan, D. C. Campbell, Matthew Campbell, Chen Jin-hua, J. C. W. Cope, Graciela Delvene, H. H. Dijkstra, Fang Zong-jie, R. N. Gardner, V. A. Gavrilova, I. A.

Goncharova, P. J. Harries, J. H. Hartman, Michael Hautmann, W. R. Hoeh, Jorgen Hylleberg, Jiang Bao-yu, P. A. Johnston, Lisa Kirkendale, Karl Kleemann, Jens Koppka, Jiří Kříž, Deusana Machado, Nikolaus Malchus, Ana Márquez-Aliaga, Jean-Pierre Masse, C. A. McRoberts, P. U. Middelfart, Simon Mitchell, L. A. Nevesskaja, Sacit Özer, John Pojeta Jr., I. V. Polubotko, Jose Maria Pons, Sergey Popov, Teresa Sánchez, A. F. Sartori, R. W. Scott, I. I. Sey, J. H. Signorelli, Vladimir Silantiev, P. W. Skelton, Thomas Steuber, J. B. Waterhouse, G. L. Wingard, & Thomas Yancey. 2011. A synoptical classification of the Bivalvia (Mollusca). University of Kansas Paleontological Contributions (online) 4:1–47.

Carter, Joseph G., C. R. Altaba, L. C. Anderson, D. C. Campbell, Fang Zongjie, P. J. Harries, & P. W. Skelton. 2015. The paracladistic approach to phylogenetic taxonomy. University of Kansas Paleontological Contributions 12:1–9.

Chartrousse, Alexandre. 1998a. The Myocardinal Organization of Coalcomaninid Rudists Revisited. Geobios Mémoire spécial 22:75–85.

Chartrousse, Alexandre. 1998b. Les Caprinidae (Rudistes) du Crétacé Inférieur. Ph.D. thesis, Université de Provence (Aix-Marseille I), Centre de Sédimentologie et Paléontologie. 281 p., 37 pl.

Chartrousse, Alexandre, & Jean-Pierre Masse. 1998. *Offneria simplex* nov. sp. (rudiste, Caprinidae) du Barrémien du Sud-Est de la France et de Cuba. Implications sur la biostratigraphie et l'évolution du genre *Offneria*. Société Géologique de France, Bulletin 169:841–850.

Chartrousse, Alexandre, & Jean-Pierre Masse. 2004. Revision of the Early Aptian Caprininae (Rudist Bivalves) of the New World. Evolutionary and Palaeobiogeographic Implications. Courier Forschungsinstitut Senckenberg 247:19–34.

Chubb, Lawrence J. 1971. Rudists of Jamaica. Palaeontographica Americana 7(45):1–257, 32 pl.

Conrad, Timothy A. 1855. Description of one Tertiary and eight Cretaceous fossils from Texas, in the collection of Major Emory. Proceedings of the Academy of Natural Sciences of Philadelphia 7:268–269.

Coogan, Alan H. 1973. New rudists from the Albian and Cenomanian of Mexico and south Texas. Revista del Instituto mexicano del Petróleo 5(2):51–83.

Coquand, Henri. 1862. Géologie et paléontologie de la région sud de la province de Constantine. Société d'Emulation de la Provence, Mémoires 2:5–342.

Cowen, Richard. 1983. Chapter 10: Algal symbiosis and its recognition in the fossil record. *In*: Michael Tevesz & P. L. McCall, eds., Biotic Interactions in Recent and Fossil Benthic Communities, Topics in Geobiology, Volume 3. Springer Science & Business Media. New York. p. 431–478.

Cox, Leslie R. 1934. On the structure of the Persian rudist genus *Trechmannella* (formerly *Polyptychus*), with the description of a new species. Malacological Society of London, Proceedings 21:42–66, 5 pl.

Damestoy, Guy. 1971. Essai de classification phylogénique des caprinidés (Lamellibranches). Muséum National d'Histoire Naturelle, Bulletin (série 2) 42: 1003–1008.

Dechaseaux, Colette. 1939. *Megalodon*, *Protodiceras*, *Diceras*, *Pachyerisma*, *Pterocardium* et l'origine des *Diceras*. Société Géologique de France, Bulletin (série 5) 9:207–218.

Dechaseaux, Colette. 1947. Bandes siphonales, piliers et siphons des rudistes. Société Géologique de France, Bulletin (série 5) 17:425–435.

Dechaseaux, Colette, L. R. Cox, A. H. Coogan, & B. F. Perkins. 1969. Superfamily Hippuritacea Gray, 1848. *In* R. C. Moore, ed., Treatise on Invertebrate Paleontology. Part N, Mollusca 6, Bivalvia, Vol. 2. The Geological Society of America & The University of Kansas Press. New York & Lawrence. p. 749–817.

Defrance, Jacques L. M. 1821. Hippurite. *In* Dictionnaire des Sciences naturelles 21. F. G. Levrault. Strasbourg. p.195–197.

Deshayes, Gérard-Paul. 1824. Dicérate. *In* Dictionnaire classique d'histoire naturelle Tome 5 (CRA-D), Rey et Gravier, Libraires-Éditeurs. Paris. p. 465–467.

Desmarest, Anselme G. 1812. Mémoire sur deux genres de coquilles fossiles cloisonnées et à siphon. Société des Sciences Physiques, Médicales et d'Agriculture d'Orléans, Bulletin 5:308–324.

Des Moulins, Charles R. A. de. 1826. Essai sur les sphérulites qui existent dans les collections de MM. F. Jouannet … et C. Des Moulins, et considérations sur la famille à laquelle ces fossiles appartiennent. Bulletin d'Histoire naturelle de la Société Linnéenne de Bordeaux 1:148–303.

Di Stefano, Giuseppe. 1889. Studi stratigrafici e paleontologici sul sistema Cretaceo della Sicilia. 1. Gli strati con Caprotina di Termini-Imerese. Atti della Reale Accademia di Scienze, Lettere e Belle Arti (new series) 10:1–44.

Douvillé, Henri. 1886. Essai sur la Morphologie des Rudistes. Société Géologique de France, Bulletin (série 3) 14:389–404.

Douvillé, Henri. 1887. Sur quelques formes peu connues de la famille des chamidés. Société Géologique de France, Bulletin (série 3) 15:756–802, 4 pl.

Douvillé, Henri. 1888. Etudes sur les caprines. Société Géologique de France, Bulletin (série 3) 16:699–730, 4 pl.

Douvillé, Henri. 1889. Sur quelques rudistes du terrain crétacé inférieur des Pyrénées. Société Géologique de France, Bulletin (série 3) 17:627–635, 2 pl.

Douvillé, Henri. 1890a. Communication sur les rudistes. Société géologique de France, Bulletin (série 3)18:324–325.

Douvillé, Henri. 1890b. Sur l'*Hippurites gosaviensis.* Société géologique de France, Bulletin (série 3) 19:xi.

Douvillé, Henri. 1896. Observations sur la charnière des lamellibranches hétérodontes. Société Géologique de France, Bulletin (série. 3) 24:26–28.

Douvillé, Henri 1911. *Pseudotoucasia* et *Bayleia.* Société Géologique de France, Bulletin (série 4) 11:190–194.

Douvillé, Henri. 1916. Le Crétacé et l'Eocène du Tibet central. Memoirs of the Geological Survey of India. Palaeontologica Indica. Vol. 5. Memoir 3. 52 p., 16 pl.

Douvillé, Henri. 1936. Les rudistes et leur évolution. Société Géologique de France, Bulletin (série 5) 5:319–358, 1 pl.

Fenerci-Masse, Mukerrem, P. W. Skelton, & Jean-Pierre Masse. 2011. The rudist bivalve genus *Gorjanovicia* (Radiolitidae, Hippuritoidea), a revision of species based on quantitative analysis of morphological characters. Palaeontology 54:1–23

Gale, Andrew S. 2000. The Cretaceous World. *In* S. J. Culver & P. F. Rawson, eds., Biotic Response to Global Change: The Last 145 Million Years. Natural History Museum & Cambridge University Press. London & Cambridge. p. 4–19.

Gili, Eulàlia, & Stefan Götz. 2018. Part N, Revised, Volume 1, Chapter 26B: Paleoecology of rudists. Treatise Online 102:1–27, 22 fig.

Gili, Eulàlia, Jean-Pierre Masse, & P. W. Skelton. 1995. Rudists as gregarious sediment-dwellers, not reef-builders, on Cretaceous carbonate platforms. Palaeogeography, Palaeoclimatology, Palaeoecology 118:245–267.

Gourrat, Christian, Jean-Pierre Masse, & P. W. Skelton. 2003. *Hypelasma salevensis* (Favre, 1913) from the Upper Kimmeridgian of the French Jura, and the origin of the rudist family Requieniidae. Geologia Croatica 56:139–148.

Gümbel, Carl W. (Ritter von). 1871. Die sogenannten Nulliporen (Lithothamnium und Dactylopora) und ihre Betheiligung an der Zusammensetzung der Kalkgesteine. Erster Theil: die Nulliporen des Pflanzenreichs (Lithothamnium). Königlich Bayerischen Akademie der Wissenschaften, Mathematisch-Physikalischen Classe, Abhandlungen 11(1)Appendix:11–52.

Harper, Elizabeth, & A. C. Checa. 2017. Physiological *versus* biological control in bivalve calcite prisms: Comparison of euheterodonts and pteriomorphs. The Biological Bulletin 232(1):19–29. doi: 10.1086/691382.

Hay, William W., R. M. DeConto, C. N. Wold, K. M. Wilson, Silke Voigt, Michael Schulz, Adrienne Wold-Rossby, W.-C. Dullo, A. B. Ronov, A. N. Balukhovsky, & Emanuel Söding. 1999. Alternative global Cretaceous paleogeography. *In* Enriqueta Barrera & C. C. Johnson, eds., The Evolution of Cretaceous Ocean/Climate Systems. Geological Society of America, Special Papers 332. Boulder, Colorado, USA. p. 1–47. http://www.odsn.de/odsn/services/paleomap/paleomap.html

Hill, Robert T. 1893. The paleontology of the Cretaceous formations of Texas: The invertebrate fossils of the *Caprina* limestone beds. Proceedings of the Biological Society of Washington 8:97–108.

Iba, Yasuhiro, & Shin-ichi Sano. 2007. Mid-Cretaceous step-wise demise of the carbonate platform biota in the Northwest Pacific and establishment of the North Pacific biotic province. Palaeogeography, Palaeoclimatology, Palaeoecology 245:462–482.

Joukowsky, Etienne, & Jules Favre. 1913. Monographie géologique et paléontologique du Salève (Haute Savoie, France). Société de Physique et d'Histoire naturelle de Genève, Mémoires 37:295-519.

Karczewski, Leon. 1969. Upper Jurassic Rudistae of the margin of the Holy Cross Mountains, Poland. Acta Palaeontologica Polonica 14:395–498.

Kauffman, Erle, & C. C. Johnson. 1988. The morphological and ecological evolution of middle and Upper Cretaceous reef-building rudists. Palaios 3:194–216.

Kennedy, W. James, & J. D. Taylor. 1968. Aragonite in rudists. Geological Society of London, Proceedings 1645:325–331.

Khazaei, Ahmad Reza, P. W. Skelton, & Mehdi Yazdi. 2010. Maastrichtian rudist fauna from Tarbur Formation (Zagros Region, SW Iran): Preliminary observations. Turkish Journal of Earth Sciences 19:703–719.

Klinghardt, Franz. 1921. Die Rudisten. Teil I. Neue Rudistenfauna aus dem Maastrichtien von Maniago (Friaul) nebst stratigraphischem Anhang. Published by the author. Berlin. 68 p.

Korbar, Tvrtko, Blanka Cvetko Tešović, Ivo Radovanović, Katarina Krizmanić, Thomas Steuber, & P. W. Skelton. 2010. Campanian *Pseudosabinia* from the Pučišća Formation on the Island of Hvar (Adriatic Sea, Croatia). Turkish Journal of Earth Sciences 19:721–731.

Kühn, Othmar. 1933. Rudistae from eastern Persia. Records of the Geological Survey of India 46:151–179.

Lamarck Jean-Baptiste de. 1799. Prodrôme d´une nouvelle classification des coquilles ... Société d'Histoire Naturelle de Paris, Mémoires 1:63–91.

Lamarck, Jean-Baptiste de. 1801. Système des animaux sans vertèbres. Published by the author. Paris. 452 p.

Lamarck, Jean-Baptiste de. 1805. Sur le dicérate, nouveau genre de coquillage bivalve. Annales du Muséum d'Histoire naturelle 6:298–302.

Lamarck Jean-Baptiste de. 1819. Histoire naturelle des animaux sans vertèbres. Tome 6 (1) Suite des Conchifères. Published by the author. Paris. 343 p.

Lan Xiu, & Wei Jingming. 1995. Late Cretaceous-Early Tertiary Marine Bivalve Fauna from the Western Tarim Basin. Science Press. 212 p., 70 pl. Chinese with English summary.

Lapeirouse, P. P. de. 1781. Description de plusieurs nouvelles espèces d'Orthocératites et d'Ostracites. Wolfgang Walther. Erlangen. 48 p.

Linnaeus, Carl. 1758. Systema Naturae per regna tria naturae, secundum classes, ordines, genera, species, cum characteribus, differentiis, synonymis, locis. Editio decima, reformata. Laurentius Salvius: Holmiae. ii, 824 p. See p. 686 for *Mercenaria mercenaria;* p. 688 for *Dosinia exoleta;* p. 691 for *Chama.*

Linnaeus Carl. 1767. Systema naturae per regna tria naturae: secundum classes, ordines, genera, species, cum characteribus, differentiis, synonymis, locis. Editio duodecima. 1. Regnum Animale. Holmiae, Laurentii Salvii. Vol. 1, part 1:21–532; part 2:533–1327. See p. 1131 for *Arctica islandica.*

Mac Gillavry, Henry. J. 1937. Geology of the Province of Camagüey, Cuba, with revisional studies in rudist paleontology. Geographische en Geologische Mededeelingen, Physiographisch-Geologische reeks 14:1–169, 10 pl.

Masse, Jean-Pierre. 1992. Les rudistes de l'Aptien inférieur d'Italie continentale: Aspects systématiques, stratigraphiques et paléobiogeographiques. Geologica Romana 28:243–260.

Masse, Jean-Pierre. 1993. Systématique, stratigraphie et paléobiogéographie du genre *Lovetchenia* (Requieniidae) du Crétacé inférieur méditerranéen. Geobios 26:699–708.

Masse, Jean-Pierre. 1996. Lower Cretaceous rudist biostratigraphy of Southern France: A Reference for Mesogean correlations. *In* Gloria Alencáster & B. E. Buitrón-Sánchez, eds., Número Dedicado a la Tercera Conferencia Internacional sobre Rudistas. Revista Mexicana de Ciencias Geológicas 12 (for 1995):236–256.

Masse, Jean-Pierre. 2002. Importance relative, chronologie et signification phylogénétique des modifications morphologiques et anatomiques chez les *Requieniidae* (rudistes) du Crétacé inférieur. *In* Mileva Sladić-Trifunović, ed., First International Conference on Rudists, Proceedings, Beograd, 1988. Union of Geological Societies of Yugoslavia, Memorial Publication. Belgrade. p. 155–171.

Masse, Jean-Pierre, Consuelo Arias, & Lorenzo Vilas. 1998. Lower Cretaceous rudist faunas of southeast Spain: An overview. *In* Jean-Pierre Masse & P. W. Skelton, eds., Quatrième Congrès International sur les Rudistes. Geobios Mémoire spécial 22:193–210.

Masse, Jean-Pierre, & Mukerrem Fenerci-Masse. 2008. Time contrasting palaeobiogeographies among Hauterivian–Lower Aptian rudist bivalves from the Mediterranean Tethys, their climatic control and palaeoecological implications. Palaeogeography, Palaeoclimatology, Palaeoecology 269:54–65.

Masse, Jean-Pierre, & Mukerrem Fenerci-Masse. 2009. *Debrunia*, a new Barremian genus of petalodontid Monopleuridae (Bivalvia, Hippuritoidea) from the Mediterranean Region. Palaeontology 52(6):1363–1372.

Masse, Jean-Pierre, Mukerrem Fenerci-Masse, Consuelo Arias, & Lorenzo Vilas. 2015. Description of a new species of *Offneria* (Hippuritida, Caprinidae) from the lower Aptian of southeast Spain. Stratigraphic, evolutionary, palaeobiogeographic and palaeoenvironmental implications. Cretaceous Research 53:153–166.

Masse, Jean-Pierre, & Magda Gallo-Maresca. 1997. Late Aptian Radiolitidae (rudist bivalves) from the Mediterranean and Southwest Asiatic regions: Taxonomic, biostratigraphic and palaeobiogeographic aspects. Palaeogeography, Palaeoclimatology, Palaeoecology 128:101–110.

Masse, Jean-Pierre, P. W. Skelton, & Teofil Slisković. 1984. *Glossomyophorus costatus* nov. gen. nov. sp., rudiste (Caprotinidae) nouveau de l'Aptien du domaine méditerranéen central et oriental. Geobios 17:723–732.

Matheron, Philippe. 1843. Catalogue méthodique et descriptif des corps organisés fossiles du Département des Bouches-du-Rhône et lieux circonvoisins. Carnaud fils. Marseille. 269 p.

Mitchell, Simon F. 2010. Revision of three large species of *Barrettia* from Jamaica. Caribbean Journal of Earth Science 41:1–16.

Mitchell, Simon F. 2013a. A revision of selected Lower Cretaceous American caprinoid rudists: Implications for phylogeny and biostratigraphy. Caribbean Journal of Earth Science 45:47–75.

Mitchell, Simon F. 2013b. A new rudist bivalve *Curtocaprina clabaughikinsorum* gen. et sp. nov. from the Middle Albian of Texas and its bearing on the origin of the Ichthyosarcolitidae Douvillé. Caribbean Journal of Earth Science 45:85–89.

Mitchell, Simon F. 2013c. Revision of the Antillocaprinidae Mac Gillavry (Hippuritida, Bivalvia) and their position within the Caprinoidea d'Orbigny. Geobios 46:423–446.

Mitchell, Simon F. 2013d. First record of a middle Cenomanian caprinuloideid rudist (Hippuritida, Bivalvia) from Montana, USA, and its geographical and stratigraphical significance. Cretaceous Research 46:59–64.

Morris, John, & John Lycett. 1850. On *Pachyrisma,* a fossil genus of lamellibranchiate Conchifera. Geological Society of London, Quarterly Journal 6:399–402.

Morris, Noel J., & P. W. Skelton. 1995. Late Campanian–Maastrichtian rudists from the United Arab Emirates-Oman border region. Bulletin of the Natural History Museum, Geology Series 51:277–305.

Munier-Chalmas, Ernest C. P. A. 1873. Prodrôme d'une Classification des Rudistes. Journal de Conchyliologie (série 3) 13(21):71–75.

Newell, Norman D. 1965. Classification of the Bivalvia. American Museum Novitates 2206:1–25.

Orbigny, Alcide d'. 1839. Note sur le genre Caprine. Revue zoologique, par la Société Cuvierienne 1839:168–170.

Orbigny, Alcide d'. 1847. Sur les Brachiopodes ou Palliobranches (deuxième mémoire). Comptes Rendus Hebdomadaires des Séances de l'Académie des Sciences 25:266–269.

Orbigny, Alcide. d'. 1850. Paléontologie française, Terrains crétacés. Tome 4, Brachiopodes. 105–328.

Orbigny, Charles-Marie d'. 1822. Notice sur quelques espèces nouvelles du département de la Charente-inférieure; la plupart recueillies à l'Ile d'Aix, par Fleuriau de Bellevue; envoyées par lui au Muséum du Jardin du Roi. Muséum d'Histoire naturelle, Mémoires 8:98–110.

Özer, Sacit. 2010a. Campanian-Maastrichtian *Pseudosabinia* from Turkey: Descriptions and taxonomic problems. Turkish Journal of Earth Sciences 19:643–669.

Özer, Sacit. 2010b. *Dictyoptychus* Douvillé: Taxonomic revision, phylogeny and biogeography. Turkish Journal of Earth Sciences 19:583–612.

Palmer, Robert H. 1933. Nuevos rudistas de Cuba. Revista de Agricultura, Comercio y Trabajo 14:95–125.

Pantoja-Alor, Jerjes, P. W. Skelton, & Jean-Pierre Masse. 2004. Barremian rudists of the San Lucas Formation around San Lucas, Michoacán, SW México. Courier Forschungsinstitut Senckenberg 247:1–17.

Parona, Carlo F. 1900. Sopra alcune rudiste senoniane dell'Appennino meridionale. Memorie dell'Accademia delle Scienze di Torino, Classe di Scienze fisiche, matematiche e naturali 50:1–23.

Parona, Carlo F. 1908. Notizie sulla fauna a rudiste della Pietra di Subiaco nella valle del'Aniene. Società Geologica Italiana, Bollettino 27:299–310.

Pascual-Cebrian, Enric, Stefan Götz, Telm Bover-Arnal, P. W. Skelton, Eulàlia Gili, Ramon Salas, & Wolfgang Stinnesbeck. 2016. Calcite/Aragonite Ratio Fluctuations in Aptian Rudist Bivalves: Correlation with Changing Temperatures. Geology 44:135–138. doi:10.1130/G37389.1

Pchelintsev, Vladimir. F. 1959. Rudists from the Mesozoic of the Crimea Mountains. Geologicheskij Musej imeni A. P. Karpinski, Akademii Nauk SSR, Serija Monograficheskaja. Moskva. 178 p., 43 pl. In Russian.

Philip, Jean. 1972. Paléoécologie des formations à rudistes du Crétacé supérieur – l'exemple du sud-est de la France. Palaeogeography, Palaeoclimatology, Palaeoecology 12:205–222.

Philip, Jean. 1981. Les rudistes du Crétacé moyen de la Province méditerranéenne occidentale. Evolution, paléoécologie, paléobiogéographie. Cretaceous Research 2:395–403.

Philip, Jean. 1986. Étude paléontologique du genre *Sabinia* (rudiste à canaux) des récifs du Campanien de Tunisie. Geobios 19:247–251.

Philip, Jean. 1998. Biostratigraphie et paléobiogéographie des rudistes: évolution des concepts et progrès récents. Société Géologique de France, Bulletin 169:689–708.

Philip, Jean, & Christine Airaud-Crumière. 1991. The demise of the rudist bearing carbonate platforms at the Cenomanian/Turonian boundary: A global control. Coral Reefs 10:115–125.

Philip, Jean, Jean Borgomano, & Salim Al-Maskiry. 1995. Cenomanian-Early Turonian carbonate platform of Northern Oman: Stratigraphy and palaeoenvironments. Palaeogeography, Palaeoclimatology, Palaeoecology 119:77–92.

Pictet, F. J. & Campiche, G. 1869. Description des fossiles du terrain Crétacé de Sainte-Croix. Matériaux pour la paléontologie suisse (5)9:1–352.

Pleničar, Mario 1961. The stratigraphic development of Cretaceous beds in southern Primorska (Slovene Littoral) and Notranjska (inner Carniola). Geologija 6:22–145.

Pons, José-Maria, & Enric Vicens. 2008. The structure of the outer shell layer in radiolitid rudists, a morphoconstructional approach. Lethaia 41:219–234.

Rao Xin, P. W. Skelton, Sha Jingeng, Cai Huawei, & Yasuhiro Iba. 2015. Mid-Cretaceous rudists (Bivalvia: Hippuritida) from the Langshan Formation, Lhasa block, Tibet. Papers in Palaeontology 1:401–424.

Regidor-Higuera, Ivan, Francisco García-Garmilla, & P. W. Skelton. 2007. Sclerochronology and diagenesis of late Cretaceous radiolitids (Bivalvia, Hippuritoidea), Spain. *In* R. W. Scott, ed., Cretaceous Rudists and Carbonate Platforms: Environmental Feedback. SEPM Special Publication 87:115–140.

Retzius, A. J. 1781. Crania oder Todtenkopfs-Muschel. Schriften der Berlinischen Gesellschaft Naturforschender Freunde 2:66–76.

Sano, Shin-ichi, Yasuhiro Iba, P. W. Skelton, Jean-Pierre Masse, Y.M. Aguilar, & Tomoki Kase. 2014. The evolution of canaliculate rudists in the light of a new canaliculate polyconitid rudist from the Albian of the Central Pacific. Palaeontology 57:951–962.

Sano, Shin-ichi, & Jean-Pierre Masse. 2013. First record of a primitive radiolitid rudist from Japan. Paleontological Research 17:317–324.

Sano, Shin-ichi, & P. W. Skelton. 2010. *Epidiceras* (Bivalvia, Hippuritoidea) from the Tithonian–Berriasian Torinosu-type Limestones of the Sakawa Area, Southwest Japan. Turkish Journal of Earth Sciences 19:733–743.

Sano, Shin-ichi, P. W. Skelton, Megumi Waterai, Yasuhiro Iba, Yasuo Kondo, & Yuichiro Sato. 2012. First record of an Early Barremian caprinid rudist from Japan: Implications for the palaeobiogeography of the Caprinidae (Bivalvia). Palaeontology 55:843–851.

Schumann, Dietrich. 2010. The morphology and function of the upper valve of *Vaccinites vesiculosus* (Woodward). Turkish Journal of Earth Sciences 19:791–798.

Scott, Robert W. 2002. Albian caprinid rudists from Texas re-evaluated. Journal of Paleontology 76:408–423.

Scott, Robert W., & H. F. Filkorn. 2007. Barremian-Albian rudist zones, U.S. Gulf coast. *In* Robert W. Scott, ed., Cretaceous Rudists and Carbonate Platforms: Environmental Feedback. SEPM Special Publication 87:167–180.

Scott, Robert W., & R. E. Hinote. 2007. Barremian-Early Aptian rudists, Sligo Formation, Texas, U.S.A. *In* Robert W. Scott, ed., Cretaceous Rudists and Carbonate Platforms: Environmental Feedback. SEPM Special Publication 87:237–246.

Scott, Robert W., Wan Xiaqiao, Sha Jingeng, & Wen Shi-Xuan. 2010. Rudists of Tibet and Tarim Basin, China: Significance to Requieniidae phylogeny. Journal of Paleontology 84:444–465.

Simo, J. A. Toni, R. W. Scott, & Jean-Pierre Masse, eds. 1993. Cretaceous carbonate platforms: An overview. Cretaceous Carbonate Platforms. AAPG Memoir 56:1–479.

Simone, Lucia, Gabriele Carannante, Daniela Ruberti, Maurizio Sirna, Giuseppe Sirna, Angela Laviano, & Marcello Tropeano. 2003. Development of rudist lithosomes in the Coniacian-Lower Campanian carbonate shelves of central-southern Italy: High-energy vs low-energy settings. Palaeogeography, Palaeoclimatology, Palaeoecology 200:5–29.

Seilacher, Adolf. 1998. Rudists as bivalvian dinosaurs. *In* P. A. Johnston & J. W. Haggart, eds., Bivalves: An Eon of Evolution. Paleontological Studies Honoring Norman D. Newell. University of Calgary Press. Calgary. p. 423–436.

Skelton, Peter W. 1974. Aragonitic shell structures in the rudist *Biradiolites*, and some palaeobiological inferences. Géologie méditérraneéne 1:63–74.

Skelton, Peter W. 1976. Functional Morphology of the Hippuritidae. Lethaia 9:83–100.

Skelton, Peter W. 1978. The evolution of functional design in rudists (Hippuritacea) and its taxonomic implications. Royal Society of London, Philosophical Transactions (series B, Biological Sciences) 284:305–318.

Skelton, Peter W. 1979. Preserved ligament in a radiolitid rudist bivalve and its implication of mantle marginal feeding in the group. Paleobiology 5:90–106.

Skelton, Peter W. 1985. Preadaptation and evolutionary innovation in rudist bivalves. Special Papers in Palaeontology 33:159–173.

Skelton, Peter W. 1988. The trans-Pacific spread of equatorial shallow-marine benthos in the Cretaceous. *In* M. G. Audley Charles & Anthony Hallam, eds., Gondwana and Tethys. Geological Society of London, Special Publication 37:247–253.

Skelton, Peter W., ed. 2003. The Cretaceous World. The Open University and Cambridge University Press. Cambridge, UK. 360 p.

Skelton, Peter W. 2013a. Rudist classification for the revised Bivalvia volumes of the 'Treatise on Invertebrate Paleontology'. Caribbean Journal of Earth Science 45:9–33.

Skelton, Peter W. 2013b. Rudist classification: Nomenclatural correction of 'Suborder Radiolitidina Skelton, 2013' to 'Suborder Hippuritidina Newell, 1965'. Caribbean Journal of Earth Science 45:34.

Skelton, Peter W., & M. J. Benton. 1993. 13. Mollusca: Rostroconchia, Scaphopoda and Bivalvia. *In* M. J. Benton, ed., The Fossil Record 2. Chapman and Hall. London. p. 237–263, 5 range charts.

Skelton, Peter W., & Eulàlia Gili. 2012. Rudists and carbonate platforms in the Aptian: A case study on biotic interactions with ocean chemistry and climate. Sedimentology 59:81–117.

Skelton, Peter W., Eulàlia Gili, Telm Bover-Arnal, Ramon Salas, & J. A. Moreno-Bedmar. 2010. A new species of *Polyconites* from the Lower Aptian of Iberia and the early evolution of polyconitid rudists. Turkish Journal of Earth Sciences 19:557–572.

Skelton, Peter W., & Jean-Pierre Masse. 1998. Revision of the Lower Cretaceous rudist genera *Pachytraga* Paquier and *Retha* Cox (Bivalvia: Hippuritacea), and the origins of the Caprinidae. Geobios Mémoire spécial 22:331–370.

Skelton, Peter W., Shin-Ichi Sano, & Jean-Pierre Masse. 2013. Rudist bivalves and the Pacific in the Late Jurassic and Early Cretaceous. Journal of the Geological Society 170:513–526.

Skelton, Peter W., & A. B. Smith. 2000. A preliminary phylogeny for rudist bivalves: Sifting clades from grades. *In* E. M. Harper, J. D. Taylor, & J. A. Crame, eds., The Evolutionary Biology of the Bivalvia. Geological Society, London, Special Publications 177:97–127.

Skelton, Peter W., & V. P. Wright. 1987. A Caribbean rudist bivalve in Oman: Island-hopping across the Pacific in the late Cretaceous. Palaeontology 30:505–529.

Sladić-Trifunović, Mileva. 1989. Pironaea-Pseudopolyconite Senonian of the Apulian Plate: Palaeobiogeographic correlations and biostratigraphy. Società Geologica Italiana, Memorie 40 (for 1987):149–162.

Smith, Andrew B. 1994. Systematics and the Fossil Record: Documenting Evolutionary Patterns. Blackwell Scientific Publications. Oxford. 223 p.

Sowerby, George B. 1834. The genera of Recent and fossil shells for the use of students in Conchology and Geology … illustrated with 264 original plates by James Sowerby. Vol. 2, pl. 91, fig. 2 (=220 in pl. series). Published by the author. London.

Sowerby, James de C. 1827. The Mineral Conchology of Great Britain; or Coloured Figures and Description of those Remains of Testaceous Animals or Shells Which Have Been Preserved at Various Times and Depths in the Earth. Meredith. London. 6:131.

Steuber, Thomas. 1999a. Isotopic and chemical intrashell variations in low-Mg calcite of rudist bivalves (Mollusca-Hippuritacea): disequilibrium fractionations and late Cretaceous seasonality. International Journal of Earth Sciences 88:551–570.

Steuber, Thomas. 1999b. Cretaceous rudists of Boeotia, central Greece. Special Papers in Paleontology 61:1–229.

Steuber, Thomas. 2000. Skeletal growth rates of Upper Cretaceous rudist bivalves: Implications for carbonate production and organism-environment feedbacks. *In* Enzo Insalaco, P. W. Skelton, & T. J. Palmer, eds., Carbonate Platform Systems: Components and Interactions. Geological Society of London, Special Publications 178:21–32.

Steuber, Thomas. 2002. Plate tectonic control on the evolution of Cretaceous platform-carbonate production. Geology 30:259–262.

Steuber, Thomas, & Martina Bachmann. 2002. Upper Aptian-Albian rudist bivalves from northern Sinai, Egypt. Palaeontology 45:725–749.

Steuber, Thomas, & Hannes Löser. 2000. Species richness and abundance patterns of Tethyan Cretaceous rudist bivalves (Mollusca: Hippuritacea) in the central-eastern Mediterranean and Middle East, analysed from a palaeontological data base. Palaeogeography, Palaeoclimatology, Palaeoecology 162:75–104.

Steuber, Thomas, Sacit Özer, Malte Schlüter, & Bilal Sari. 2009. Description of *Paracaprinula syriaca* Piveteau (Hippuritoidea, Plagioptychidae) and a revised age of ophiolite obduction on the African-Arabian Plate in southeastern Turkey. Cretaceous Research 30:41–48.

Steuber, Thomas, & Malte Schlüter. 2012. Strontium-isotope stratigraphy of Upper Cretaceous rudist bivalves: Biozones, evolutionary patterns and sea-level change calibrated to numerical ages. Earth-Science Reviews 114:42–60.

Steuber, Thomas, R. W. Scott, S. F. Mitchell, & P. W. Skelton. 2016. Part N, Revised, Volume 1, Chapter 26C: Stratigraphy and diversity dynamics of Jurassic–Cretaceous Hippuritida (rudist bivalves). Treatise Online 81:1–17, 7 fig., 1 table.

Swinburne, Nicola H. M., & Jean-Pierre Masse. 1995. Early Cretaceous rudist fauna of Allison and Resolution guyots, Mid-Pacific Mountains. *In* E. L. Winterer, W. W. Sager, J. V. Firth, & J. M. Sinton, eds., Proceedings of the Ocean Drilling Program, Scientific Results 143:3–14.

Tišlar, Josip, Igor Vlahović, Ivo Velić, Dubravko Matičec, & Julie Robson. 1998. Carbonate facies evolution from the Late Albian to Middle Cenomanian in southern Istria (Croatia): Influence of synsedimentary tectonics and extensive organic carbonate production. Facies 38:137–152.

Tompa, Alex S., & Norimitsu Watabe. 1976. Ultrastructural investigation of the mechanism of muscle attachment to the gastropod shell. Journal of Morphology 149:339–351.

Toucas, Aristide. 1904. Études sur la classification et l’évolution des Hippurites, deuxième partie. Société géologique de France, Paléontologie, Mémoires 30:65–128.

Toucas, Aristide. 1909. Etudes sur la classification et l’évolution des Radiolitidés: *Sauvagesia* & *Biradiolites.* Société géologique de France, Paléontologie, Mémoires 36:79–132.

Trechmann, Charles T. 1924. The Cretaceous limestones of Jamaica and their Mollusca. Geological Magazine 61:385–410.

Vermeij, Geerat J. 2013. The evolution of molluscan photosymbioses: a critical appraisal. Biological Journal of the Linnean Society 109:497–511.

Vermunt, L. W. J. 1937. Cretaceous rudists of Pinar del Rio province, Cuba. Journal of Paleontology 11:261–275.

Vogel, Klaus. 1960. Zu Struktur und Funktion der ‘Siphonalpfeiler’ der Hippuriten (Lamellibranchiata). Paläontologisches Zeitschrift 34:275–294.

Vogel, Klaus. 1975. Endosymbiotic algae in rudists? Palaeogeography, Palaeoclimatology, Palaeoecology 17:327-332.

Vogel, Klaus. 1978. Function of pallial canals of Caprinidae (rudists, Pelecypoda). Neues Jahrbuch für Geologie und Paläontologie, Abhandlungen 157:159–163.

White, Charles A. 1885. On new Cretaceous fossils from California. U. S. Geological Survey, Bulletin 22:7–14.

Whitfield, Robert P. 1897. Descriptions of species of rudistae from the Cretaceous rocks of Jamaica, W. I., collected and presented by Mr. F. C. Nicholas. American Museum of Natural History, Bulletin 9(12):185–196.

Woodward, Samuel P. 1855. On the structure and affinities of the Hippuritidae. Quarterly Journal of the Geological Society 11:40–61.

Yabe, Hisakatsu, & Takumi Nagao 1926. *Praecaprotina,* nov. gen. from the Lower Cretaceous of Japan. Science Reports of the Tohoku Imperial University (series 2) 9:21–24.

Yanin, Boris T. 1989. The Jurassic and Cretaceous Rudists: Stratigraphical and Geographical Distribution. Nauka. Moskva. 214 p., 16 pl. In Russian.

Yanin, Boris T. 1990. Kriterii sistematiki rudistov. *In* V. V. Menner, ed., Sistematika i Filogeniia Bespozvonochikh. Kriterii Vydeleniia Vyschikh Taksonov. Nauka. Moscow. p. 57–69. In Russian.

Yanin, Boris T. 1995. The system, phylogeny and evolution of rudists. Palaeontological Institute of the Russian Academy of Sciences. Moscow. 228 p. In Russian.

Yonge, C. Maurice. 1967. Form, habit and evolution in the Chamidae (Bivalvia) with reference to conditions in the rudists (Hippuritacea). Royal Society of London, Philosophical Transactions (series B, Biological Sciences) 252(775):49–105.

Zapfe, Helmuth. 1937. Paläobiologische Untersuchungen an Hippuritenvorkommen der nordalpinen Gosauschichten. Verhandlungen der Zoologisch-Botanischen Gesellschaft in Wien 86/87:73–124.